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Caryopsis Morphology and Classification in the Triticeae (Pooideae: Poaceae)

EDWARD E. TERRELL
and
PAUL M. PETERSON

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Edward E. Terrell and Paul M. Peterson

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ABSTRACT

Terrell, Edward E., and Paul M. Peterson. Caryopsis Morphology and Classification in the Triticeae (Pooideae: Poaceae). *Smithsonian Contributions to Botany*, number 83, 25 pages, 12 figures, 3 tables, 1993. Detailed descriptions and drawings of caryopses are presented for 35 species representing 18 genera in the Triticeae. We studied the morphological variation in non-embryo characters involving the length, shape, compression, lateral ridges, sulcus development, coronas, and apical hairs of the caryopsis. Based on shared characters of the caryopses, we recognize three groups of genera as two major subtribes and one monogeneric subtribe. The Hordeinae includes *Agropyron, Crithopsis, Elymus, Elytrigia, Eremopyrum, Hordelymus, Hordeum, Leymus, Psathyrostachys,* and *Taeniatherum;* Triticinae includes *Aegilops, Amblyopyrum, Dasypyrum, Heteranthelium, Secale,* and *Triticum;* and Henrardiinae includes *Henrardia.* Similarities among the caryopses of 14 species of *Elymus, Elytrigia, Leymus,* and *Psathyrostachys* support a broad interpretation of *Elymus.* The caryopses of *Brachypodium* resemble those of the genera in the Hordeinae and to some extent *Bromus.*

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Caryopsis Morphology and Classification in the Triticeae (Pooideae: Poaceae)

Edward E. Terrell
and Paul M. Peterson

Introduction

The Triticeae* is one of the smaller tribes of grasses (approximately 330 species), but the most economically important, including wheat (*Triticum*), barley (*Hordeum*), rye (*Secale*), and some important forage grasses in *Elymus* and *Agropyron*. This tribe has been subjected to more varied classifications than any other tribe of grasses. One extreme view, based on successful hybridizations among the genera, advocated the recognition of a single genus (Stebbins and Walters, 1949). Löve (1984) recognized 37 genera by assigning generic status to each unique genomic formula. Most of the recent reorganizations within the Triticeae have occurred in the large genera, *Elymus* and *Agropyron*. *Agropyron* sens. str. now includes only the crested wheatgrass complex, centered around *A. cristatum*, and *Elymus* has been split into several genera (Tzvelev, 1976:147–203, 253–276; Melderis, 1978b, 1980; Dewey, 1982, 1983a,b, 1984; Barkworth et al., 1983; Barkworth and Atkins, 1984; Barkworth and Dewey, 1985; Löve, 1982, 1984; Baum 1977; Baum et al., 1991). On the other hand, Estes and Tyrl (1982) have argued for a broader circumscription by including many segregate genera within *Elymus*. More recently the genomic and alternative classifications of the Triticeae have been addressed by Gupta and Baum (1986), Baum et al. (1987), Jauhar and Crane (1989), and Kellogg (1989).

Non-embryo characters of the caryopses have been neglected by researchers, yet they can offer important information on phylogenetic relationships. At least within some groups, the caryopses may be an important part of the grass flower for taxonomy. Characteristics of the caryopses other than the embryo have been investigated by certain authors, e.g., Martin (1946), Yakovlev (1950), Kuwabara (1962), Bogdan (1966), Terrell (1971), Rosengurtt et al. (1971), Watson and Clifford (1976), Koch (1979), and MacFarlane and Watson (1980, 1982). Other papers included a survey of non-embryo characteristics within a genus or tribe, e.g., Bayles and Clark (1954) on *Triticum;* Colbry (1957) on *Sporobolus;* Reeder (1965) on Orcuttieae; Kowal and Rudnicka-Sternowa (1969) on *Bromus;* and Brandenburg et al. (1991) on *Diarrhena*.

The purposes of the present study are to evaluate the morphological structure of the caryopses within the Triticeae and to determine the importance of non-embryo characters in the classification of this tribe.

MATERIALS AND METHODS.—Caryopses of 35 species belonging to 18 genera of Triticeae were obtained from plants grown at the United States Department of Agriculture (USDA) facilities or from herbarium specimens at the United States National Herbarium (US) or the Royal Botanic Gardens, Kew (K). Specimens from the USDA usually have Plant Introduction (PI) numbers or Cereal Investigation (CI) numbers. The CI numbers are used for well-known crops and are materials derived from cultivated plots at USDA field stations. The sources of our material follow each species' caryopses description. Voucher specimens and caryopses are deposited at US. We selected genera and species that would provide representative samples of the variation present in the Triticeae. The type species and other species representing different sections of a genus were included when possible. The samples were compared with other collections of the same species to confirm their identities. We were unable to obtain mature caryopses of the recently described genera, *Festucopsis* (C.E. Hubbard) Melderis (Melderis, 1978a), native to Albania and Greece, and *Kengyilia* Yen & Yang (Yen and Yang, 1990),

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* *Authors of scientific names are given in text or tables.*

native to China.

Mature, dry caryopses were examined with a low-power stereo microscope and the most important characters were described for each species. When available, more than one accession was examined to study the variation, and additional accessions were drawn for certain species to show the variation. Consequently, the description and illustration for each species were derived from one to several accessions. The caryopses were drawn in four aspects: ventral, lateral, and dorsal views; and transverse section.

Scanning electron microscopy (SEM) was conducted by direct mounting of the dry caryopsis on an aluminum stub and coating with gold palladium. Samples were then examined using SEM and photographed.

The working classification adopted for the purpose of study arranges the genera according to genome (Table 1) starting with *Elymus* and includes the sometimes segregated genera *Elytrigia, Leymus,* and *Psathyrostachys. Elymus* is employed in a rather restricted sense and *Aegilops* and *Triticum* are treated as distinct. *Sitanion* and *Hystrix* are tentatively included in *Elymus* because they share the same genome (Dewey, 1984:246–250; Löve, 1982, 1984:447). *Henrardia* is included in the tribe in agreement with Hubbard (1946) and recent literature. *Brachypodium* is added to this study because Clayton and Renvoize (1986) included the genus in their treatment of the Triticeae and Macfarlane and Watson (1982) and Kellogg (1989) have recognized the genus as a sister group to the tribe.

ACKNOWLEDGMENTS.—We dedicate this paper to Regina O. Hughes in recognition of her long and distinguished career as a botanical artist, as well as for her accurate and artistic drawings that are presented here. Financial support during early parts of the study was provided by the Agricultural Research Service, USDA, Beltsville, Maryland. We would like to thank G.A. White, USDA Plant Introduction Office, D.H. Smith, Jr., National Small Grain Collection, USDA, and S.A. Renvoize, Royal Botanic Gardens, Kew, for providing material for study. A. Tangerini assisted with the illustrations and M.T. Strong aided in the preparation of the literature cited. Access to the scanning electron microscopy equipment at USDA was provided by W.P. Wergin. We also thank J.R. Estes, S. Frederiksen, and T.D. Pizzolato for suggesting important modifications that significantly improved the manuscript.

TABLE 1.—Genera and species examined, genome, and figure number.

Taxon	Genome	Figure
ELYMOID GROUP		
Elymus sibiricus	SH	2
E. dahuricus	SH	2
E. caninus	SH	2
E. hystrix	SH	2
E. elymoides	SH	3
E. distichus	J, JE	3
Elytrigia repens	SX, S, E, J	3
E. elongata	E	3
E. spicata	S	4
Leymus arenarius	JN	4
L. angustus	JN	4
L. alaicus subsp. *karataviensis*	JN	4
Psathyrostachys juncea	N	5
P. fragilis	N	5
Hordeum bogdanii	H	5
H. jubatum	H	5
H. pusillum	H	1
H. spontaneum	I	6
H. distichon	I	6
H. vulgare	I	6
Agropyron cristatum	P	7
Eremopyrum triticeum	F	7
Crithopsis delileana	K	8
Hordelymus europaeus	HT	8
Taeniatherum caput-medusae	T	8
TRITICINOID GROUP		
Aegilops cylindrica	CD	9
A. triuncialis	CU	10
Amblyopyrum muticum	Z	10
Triticum monococcum	A	11
T. dicoccon	AB	11
T. aestivum	ABD	11
Secale cereale	R	11
Dasypyrum villosum	V	12
Heteranthelium piliferum	Q	12
HENRARDIOID GROUP		
Henrardia persica	O	12
BRACHYPODIUM GROUP		
Brachypodium pinnatum	–	12

Results

NON-EMBRYO CHARACTERS AND THEIR VARIATION.—The non-embryo morphological characters determined to be the most important for revealing relationships among the genera are as follows: caryopsis length and shape; type of compression, whether dorsiventral, dorsiventral with compressed ventral face only, lateral, or none; extent of compression; presence or absence of lateral ridges and the extent of their development; sulcus depth and width and their extent; whether sulcus is widened distally; corona length and whether vertical or cap-like; density and length of apical hairs; and embryo length relative to caryopsis length.

The Triticeae have relatively large caryopses ranging from (2.5–) 3.5–11 mm long in the species studied. Shapes of these in outline varied from oblanceolate or oblong to lanceolate, elliptic, or ovate. The most common compression is moderately to strongly dorsiventral, but compression varies to none or to slightly or strongly laterally compressed. Compression is differential in *Aegilops cylindrica* and *A. triuncialis* (Figures 9, 10), in which the caryopses are flattened on the ventral face and rounded on the dorsal face. An additional character is the presence of low lateral ridges extending longitudinally that are visible in transverse sections. These occur in *Crithopsis, Hordelymus,* and *Taeniatherum* (Figure 8) and are very small

or obscure in certain species of *Elymus* (Figure 3*d*). Another important character is the presence or absence of a sulcus (Bayles and Clark, 1954; Stearn, 1973), also called the furrow or groove. Depth of the sulcus varies from shallow to deep. Its margins may be flattened or more often form a rim, as in *Elymus* (Figures 2*e–m*, 3*a–d*). The width of the sulcus varies from wide and broadly U-shape to narrow or entirely closed by the fusion of the margins. The sulcus may be wider toward the apex of the caryopsis, particularly in *Elymus* (Figure 2*e–m*). Both faces of the caryopsis may be strongly compressed and the sulcus very shallow (e.g., *Henrardia*, Figure 12*j–m*).

The small membranous corona is attached to the apex of the caryopsis and varies from whitish to yellowish. The corona may be partly concealed by the apical hairs. In *Triticum* relatives, especially *Dasypyrum* (formerly *Haynaldia*) and *Heteranthelium*, the corona is a smooth or angulate cap (Figure 12*a–d*). Apical hairs range from long to short and may densely or sparsely cover the surface. The apex may be glabrous or glabrate in some individuals of *Dasypyrum*, *Heteranthelium*, *Hordeum distichon*, *H. vulgare*, and *Secale cereale*.

Embryo lengths in species studied varied from ($^2/_5$–) $^1/_3$–$^1/_5$ (–$^1/_6$) as long as the caryopsis (all measurements include the apical hairs). When viewed under low power the embryo and adjacent areas seem to show some variation among the taxa, but further examination would require special methods that were not included in this study.

Scanning electron microscopy of the caryopsis of *Hordeum pusillum* shows the shape, relative size of the embryo, and details of the unicellular tapering apical cells (Figure 1*a–c*). Also shown is the spermoderm or outer coat (Figure 1*a*), which some authors have utilized for distinguishing genera or species (e.g., Körber-Grohne, 1981; Buth, 1982; Jordan et al., 1983). Under low magnification we did not see any conspicuous differences in the spermoderms of the Triticeae reviewed for this study.

DESCRIPTIONS OF CARYOPSES.—Morphological descriptions of the caryopsis and background data are given starting with *Elymus* (Table 1). Each description is accompanied by the accepted name, synonyms, genome, chromosome number, and geographical distribution; sometimes recent classifications and comments are added. It should be especially noted that each description may be based on accessions additional to the one illustrated. Genomes and chromosome numbers are in brackets. Main sources for the data on genomes were taken from Dewey (1984) and Löve (1984); for chromosome numbers Tzvelev (1976), Melderis (1978b, 1980), Dewey (1982), and Löve (1984); for geographic distribution Hitchcock (1951) and Tzvelev (1976). The source for each collection is given and the illustrated collection(s) is marked with an asterisk if more than one accession is listed. More detailed collection data can be provided on request.

For some characters subjective terms such as dense or sparse are employed. In order to provide a reference point, the following terms are exemplified by citing a particular species along with a specific figure in the illustrations. The extent of compression of the caryopses is given as slight (*Eremopyrum triticeum*, Figure 7*l,p*), moderate (*Elymus sibiricus*, Figure 2*d*), or strong (*Crithopsis delileana*, Figure 8*d*). Sulcus depth is recorded as shallow (*Elymus sibiricus*, *E. dahuricus*, *E. caninus*, and *E. hystrix*, Figure 2), medium (*Eremopyrum triticeum*, Figure 7*l,q*), or deep (*Triticum dicoccon*, Figure 11*h*). Sulcus widths are recorded as wide (*Elytrigia spicata*, *Leymus arenarius*, and *L. alaicus*, Figure 4*d,h,p*), medium (*Eremopyrum triticeum*, Figure 7*p,q*), narrow (*Hordeum distichon*, Figure 6*h*), or very narrow or closed (*Aegilops cylindrica*, *Triticum monococcum*, *T. dicoccon*, and *T. aestivum*, Figures 9*d,e,o*, 11*d,h,l*). The sulcus is sometimes wider distally, i.e., toward the apex in *Elymus dahuricus* and *E. caninus* (Figure 2*e,i*). The density of apical hairs on the corona is categorically determined to be either dense (*Elymus sibiricus*, *E. dahuricus*, *E. caninus*, *E. hystrix*, and *E. elymoides*, Figure 2*c,g,k,p*) or sparse (*Eremopyrum triticeum*, Figure 7*k,o*). Length of apical hairs is considered short (*Brachypodium pinnatum*, Figure 12*n*), medium (*Hordeum jubatum*, Figure 5*m,n,o*), or long (*Elymus hystrix*, Figure 2*n,o,p*).

Elymus sibiricus Linnaeus [*Clinelymus sibiricus* (Linnaeus) Nevski] [SH; 2n = 28]. The type species of *Elymus*, occurs from Ural region and Baltic region to eastern Asia and northwest North America.

Caryopses: 5–5.5 mm long; oblanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none; sulcus shallow, medium, or wide; corona ~0.5 mm long; apical hairs dense, length medium; embryo $^1/_5$–$^1/_6$ as long as caryopsis (Figure 2*a–d*). (**PI 362191*, Mongolia; *K.M. Liou L428*, China (US); *PI 326267* and *PI 370673*, cultivated at Vavilov Institute, St. Petersburg, Russian Federation.)

Elymus dahuricus Turczaninow ex Grisebach [*Clinelymus dahuricus* (Turczaninow ex Grisebach) Nevski] [SH; 2n = 28, 42]. Placed in *Elymus* sect. *Turczaninovia* (Nevski) Tzvelev by Tzvelev (1976:157). It occurs from Iran to eastern Asia.

Caryopses: 4.5–5.5 mm long; oblanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none; sulcus shallow, wide throughout or medium at base and widened distally; corona 0.5–1 mm long; apical hairs dense, length medium; embryo $^1/_5$ as long as caryopsis (Figure 2*e–h*). (*PI 314680*, Uzbekistan.)

Elymus caninus (Linnaeus) Linnaeus [*Agropyron caninum* (Linnaeus) P. Beauvois; *Roegneria canina* (Linnaeus) Nevski] [SH; 2n = 28]. Native to Europe and temperate Asia, traditionally it has been in *Agropyron* but was placed in *Elymus* sect. *Goulardia* (Husnot) Tzvelev by Tzvelev (1976:158) and Melderis (1978b, 1980).

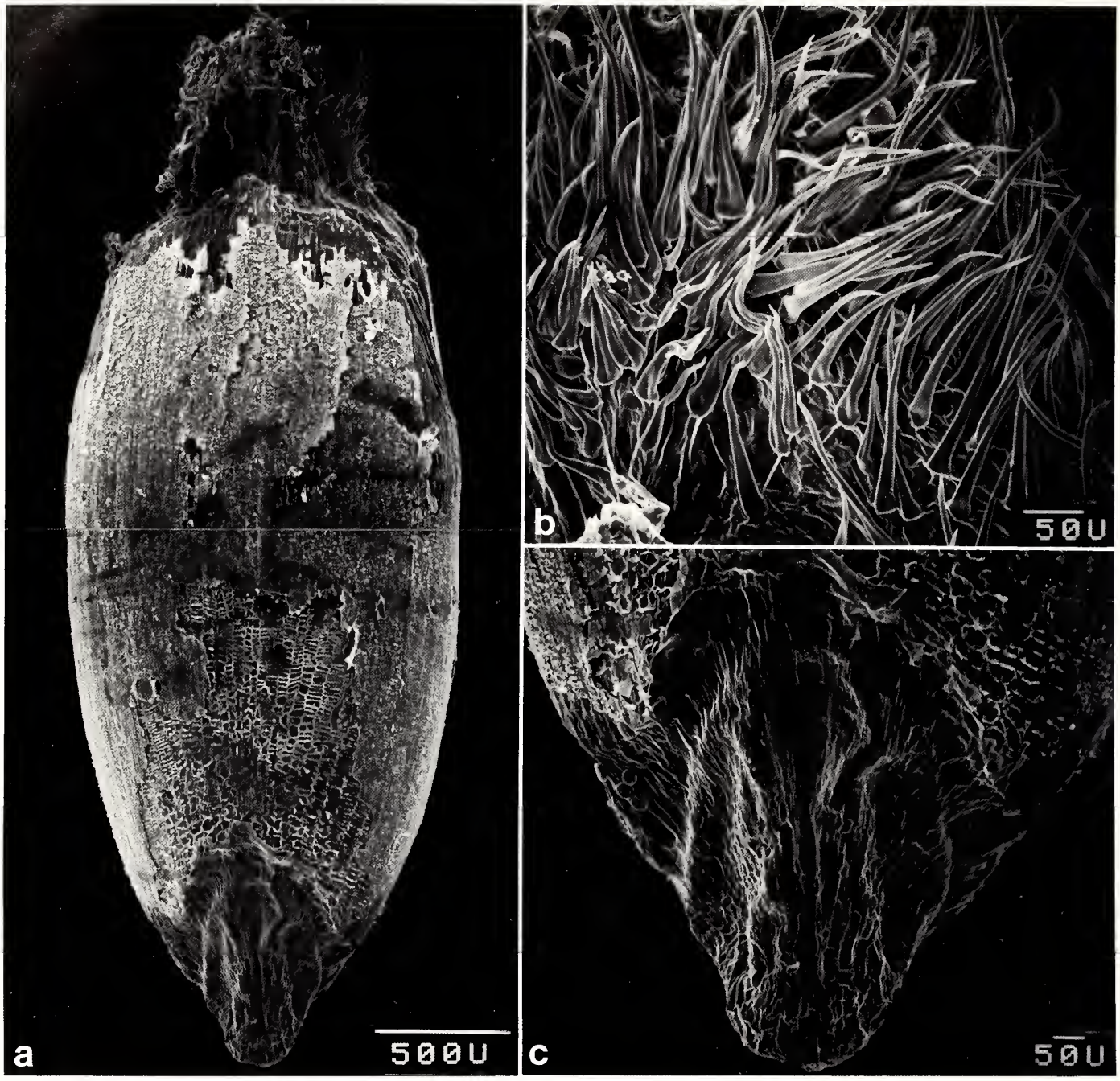

FIGURE 1.—Scanning electron micrographs of the caryopsis of *Hordeum pusillum*. (Scale bars: a = 500μm; b,c = 50μm.)

Caryopses: 5–6 mm long; oblanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none; sulcus shallow, wide throughout or medium at base and widened distally; corona 0.5–1 mm long; apical hairs dense, length medium; embryo 1/5 as long as caryopsis (Figure 2*i–m*). (*PI 314616*, Uzbekistan.)

Elymus hystrix Linnaeus [*Hystrix patula* Moench] [SH; 2n = 28]. It occurs in eastern Canada and eastern and central United States.

Caryopses: 5.5–6 mm long; oblanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none; sulcus shallow, wide throughout or

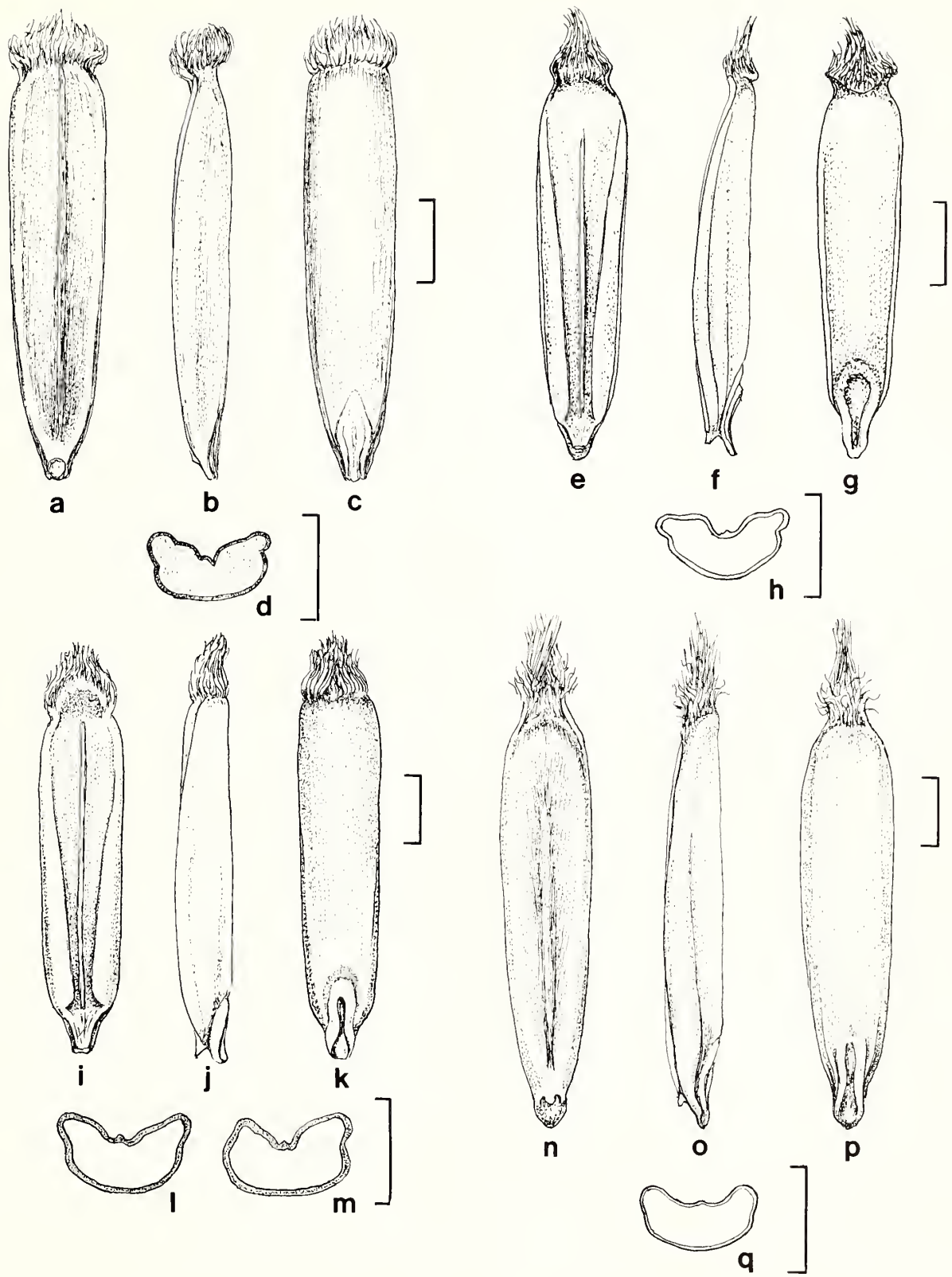

FIGURE 2.—Caryopsis of *Elymus sibiricus* (*a–d*); *Elymus dahuricus* (*e–*h); *Elymus caninus* (*i–m*); and *Elymus hystrix* (*n–q*). Ventral views (*a,e,i,n*); lateral views (*b,f,j,o*); dorsal views (*c,g,k,p*); transverse sections (*d,h,l,m,q*). (All scale bars = 1 mm.)

medium at base and widened distally; corona 0.8–1.2 mm long; apical hairs dense, long; embryo 1/4 as long as caryopsis (Figure 2*n–q*). (*Terrell & Meyer 4318,* Perry Co., Indiana.)

Elymus elymoides (Rafinesque) Swezey [*Sitanion hystrix* (Nuttall) J.G. Smith] [SH; 2n = 28]. Native in central and western United States and western Canada.

Caryopses: 5–6 mm long; oblanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges rudimentary; sulcus shallow to medium, wide throughout or medium at base and widened distally; corona 0.5–1 mm long; apical hairs dense, length short to medium; embryo 1/5 as long as caryopsis (Figure 3*a–d*). (*Terrell & Wheeler s.n.,* 6 Jul 1978, Rosebud Co., Montana.)

Elymus distichus (Thunberg) Melderis [*Agropyron distichum* (Thunberg) P. Beauvois; *Thinopyrum distichum* (Thunberg) A. Löve] [J fide Löve, 1984:476, JE fide Dewey, 1984:274; 2n = 28]. Native to South Africa.

Caryopses: 9–10.5 mm long; lanceolate, narrowly elliptic; compression dorsiventral, moderate to strong, dorsal face rounded, lateral faces narrow; lateral ridges none; sulcus medium to deep, wide throughout; corona 1–2 mm long, conspicuous, wider than apex of caryopsis (drawing shows fragile styles); apical hairs sparse to dense, short; embryo 1/4–1/5 as long as caryopsis (Figure 3*e–h*). (*K.C. Johnson s.n.,* Feb 1977, coast of Western Cape, Republic of South Africa, via USDA.)

Elytrigia repens (Linnaeus) Nevski subsp. *repens* [*Agropyron repens* (Linnaeus) P. Beauvois; *Elymus repens* (Linnaeus) Gould] [SX fide Dewey, 1984:276; E, J, and S fide Löve, 1984:484; 2n = 42, also 28, 56]. This species, the type of *Elytrigia,* traditionally was placed in *Agropyron.* It was assigned to *Elymus* sect. *Elytrigia* (Desvaux) Melderis by Melderis (1978b). It occurs in Europe, Asia, North Africa, and as a weed in North America, South America, and Australia (Bor, 1968:220, 221; Tzvelev, 1976:196).

Caryopses: 4.5–5.5 mm long; oblong; compression dorsiventral, slight, dorsal face rounded; lateral ridges none; sulcus depth shallow to medium, width medium at base and slightly widened distally; corona 0.5–1 mm long; apical hairs dense, short; embryo 1/4–1/5 as long as caryopsis (Figure 3*i–l*). (*Dewey s.n.,* Apr 1972, Utah, via USDA.)

Elytrigia elongata (Host) Nevski subsp. *elongata* [*Agropyron elongatum* (Host) P. Beauvois; *Lophopyrum elongatum* (Host) A. Löve; *Thinopyrum elongatum* (Host) D.R. Dewey; *Elymus elongatus* (Host) Runemark] [E; 2n = 14]. Occurs in Mediterranean region to southwest and probably central Asia. It was traditionally in *Agropyron* but was placed in *Elytrigia* sect. *Caespitosae* (Rouy) Tzvelev (Tzvelev, 1976:194, 195) and in *Elymus* sect. *Caespitosae* (Rouy) Melderis (Melderis, 1978b).

Caryopses: 5–6.5 mm long; oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none; sulcus shallow, wide throughout or medium at base and widened distally; corona 0.5–1 mm long; apical hairs dense, short; embryo 1/4 as long as caryopsis (Figure 3*m–p*). (*PI 264770,* Germany.)

Elytrigia spicata (Pursh) D.R. Dewey [*Agropyron spicatum* (Pursh) Scribner & Smith; *Pseudoroegneria spicata* (Pursh) A. Löve; *Elymus spicatus* (Pursh) Gould] [S; 2n = 14, 28]. Ranges from central and western North America to Alaska. Traditionally in *Agropyron,* it has been placed in *Elymus* sect. *Caespitosae* (Rouy) Melderis (Melderis, 1978b) or *Elytrigia* sect. *Caespitosae* (Rouy) Tzvelev (Tzvelev, 1976) or in *Pseudoroegneria* (Nevski) Löve.

Caryopses: 4–5.5 mm long; oblong or narrowly elliptic; compression dorsiventral, strong to moderate, dorsal face slightly rounded; lateral ridges none; sulcus deep, wide throughout; corona 0.5–1 mm long; apical hairs dense, length medium; embryo 1/4–1/5 as long as caryopsis (Figure 4*a–d*). (**Terrell 4783,* Davis Co., Utah; *Terrell s.n.,* 26 Jul 1977, Bingham Co., Idaho; *Terrell & Wheeler s.n.,* 7 Jul 1978, Rosebud Co., Montana.)

Leymus arenarius (Linnaeus) Hochstetter [*Elymus arenarius* Linnaeus] [JN; 2n = 56]. This type species occurs in Europe and eastern Europe.

Caryopses: 7–8.5 mm long; oblanceolate or oblong; compression dorsiventral, moderate to strong, dorsal face flattened to somewhat rounded, lateral faces sometimes flattened; lateral ridges none; sulcus depth medium, wide; corona 1–2 mm long; apical hairs dense, long; embryo 1/4 as long as caryopsis (Figure 4*e–h*). (**PI 316233,* cultivated in Russian Federation; *PI 345979,* Norway.)

Leymus angustus (Trinius) Pilger [*Elymus angustus* Trinius] [JN; 2n = 28, 42, 56, 84]. Occurs in central Asia and Siberia. It was classified in *Leymus* sect. *Aphanoneuron* (Nevski) Tzvelev by Tzvelev (1976:263, 264).

Caryopses: 7.5–8.5 mm long; oblong or lanceolate; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none or inconspicuous; sulcus depth medium, width medium to wide; corona 1–2 mm long; apical hairs dense, long; embryo 1/5 as long as caryopsis (embryo area bearing short, sparse hairs) (Figure 4*i–l*). (*PI 271893,* USSR, via Canada.)

Leymus alaicus subsp. *karataviensis* (Roshevits) Tzvelev [*Elymus karataviensis* Roshevits; *Elymus alaicus* Korsh, sens. lat.; *Aneurolepidium karataviense* (Roshevits) Nevski] [JN; 2n = 28]. Native to central Asia. Nevski (1934:704) placed it in *Aneurolepidium* and Tzvelev

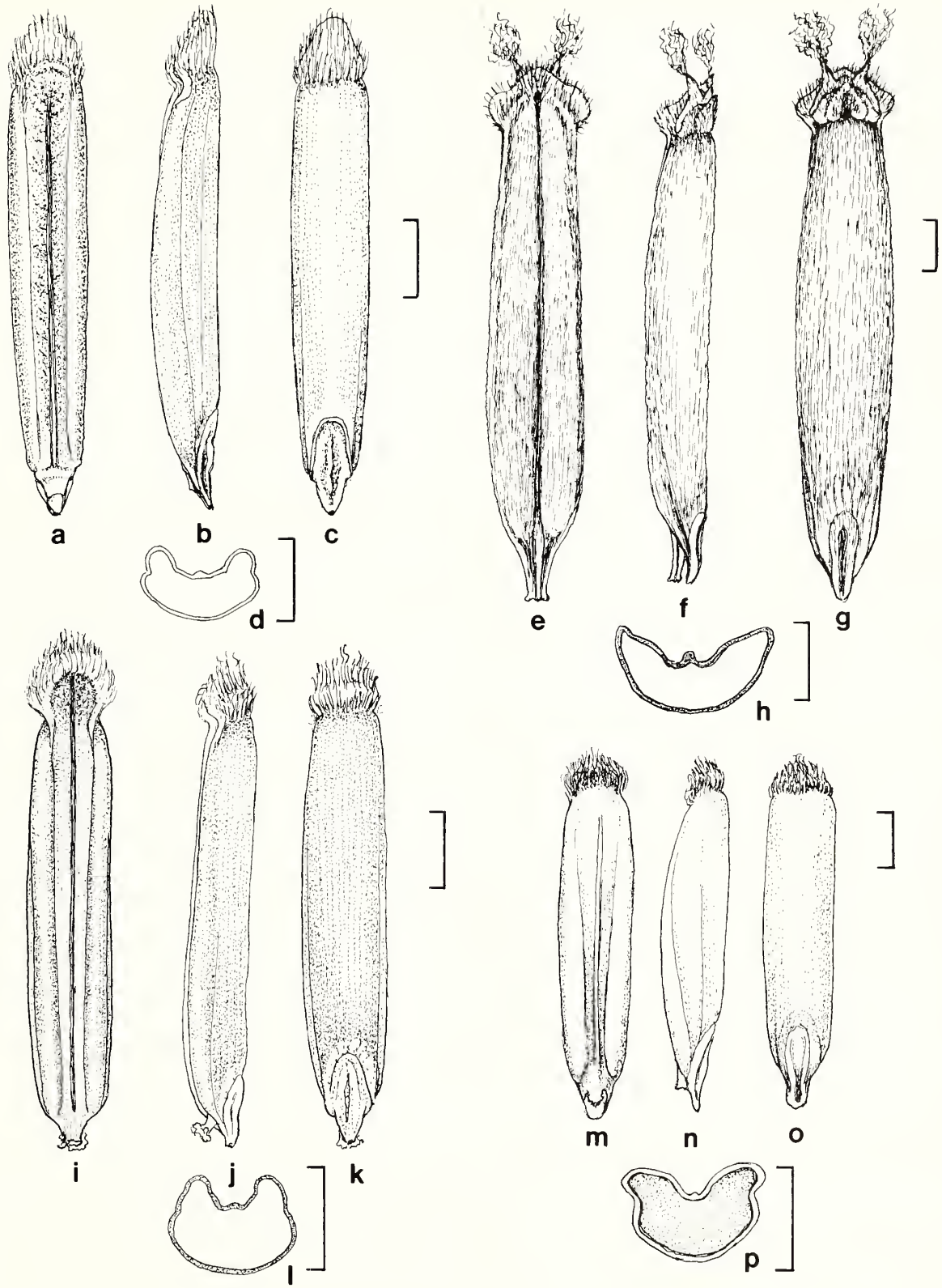

FIGURE 3.—Caryopsis of *Elymus elymoides* (*a–d*); *Elymus distichus* (*e–h*); *Elytrigia repens* (*i–l*); and *Elytrigia elongata* (*m–p*). Ventral views (*a,e,i,m*); lateral views (*b,f,j,n*); dorsal views (*c,g,k,o*); transverse sections (*d,h,l,p*). (All scales = 1 mm.)

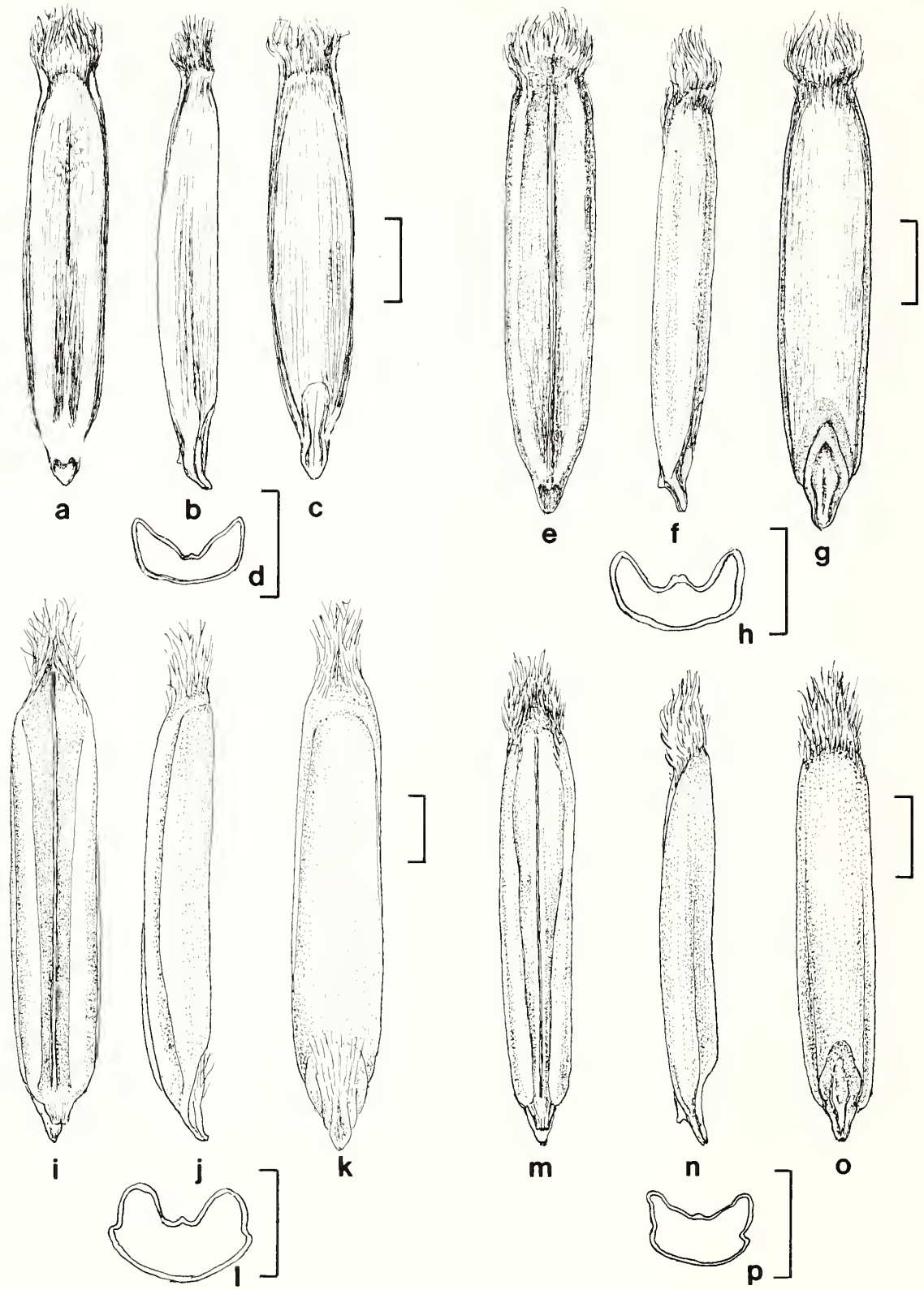

FIGURE 4.—Caryopsis of *Elytrigia spicata* (*a–d*); *Leymus arenarius* (*e–h*); *Leymus angustus* (*i–l*); and *Leymus alaicus* subsp. *karataviensis* (*m–p*). Ventral views (*a,e,i,m*); lateral views (*b,f,j,n*); dorsal views (*c,g,k,o*); transverse sections (*d,h,l,p*). (All scales = 1 mm.)

(1976:263, 264) put it in *Leymus* sect. *Aphanoneuron* (Nevski) Tzvelev.

Caryopses: 5–6 mm long; oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges very small; sulcus depth shallow to medium, width medium to wide, widened distally; corona 0.5–1 mm long; apical hairs dense, length medium to long; embryo 1/4–1/5 as long as caryopsis (Figure 4*m–p*). (*PI 314671,* USSR.)

Psathyrostachys juncea (Fischer) Nevski [*Elymus junceus* Fischer] [N; 2n = 14]. Ranges from eastern Europe to central Asia, Tibet, and Mongolia.

Caryopses: 4–5 mm long; oblanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges none or small; sulcus depth medium, width medium to wide; corona 0.5–1 mm long; apical hairs dense, length medium; embryo 1/4–1/5 as long as caryopsis (Figure 5*a–d*). (**PI 314082,* Stavopol Botanical Garden, Russian Federation; *PI 370672,* Uzbekistan; *PI 314668,* Uzbekistan.)

Psathyrostachys fragilis (Boissier) Nevski [*Elymus fragilis* (Boissier) Grisebach; *Hordeum fragile* Boissier] [N; 2n = 14]. Native to Asia Minor and southwest Asia.

Caryopses: 6.5–7.5 mm long; oblong; compression dorsiventral, moderate, dorsal face rounded; lateral ridges very small; sulcus depth medium, width medium to wide; corona 0.5–1 mm long; apical hairs dense, length medium to short; embryo 1/5 as long as caryopsis (Figure 5*e–h*). (*Dewey 1186,* CL 33-17, Iran, via USDA.)

Hordeum bogdanii Wilensky [*Critesion bogdanii* (Wilensky) A. Löve] [H; 2n = 14]. Native in Transvolga, lower Don, and lower Volga regions to Tibet and Mongolia. Placed in *Hordeum* subg. *Hordeastrum* (Doell) Rouy by Tzvelev (1976:281–283).

Caryopses: 4.5–5.0 mm long; oblong or lanceolate; compression dorsiventral, moderate to strong, dorsal face somewhat rounded; lateral ridges none; sulcus shallow to medium, width medium; corona ~0.5 mm long; apical hairs dense, width medium; embryo 1/4–1/5 as long as caryopsis (Figure 5*i–l*). (*PI 269406,* Afghanistan.)

Hordeum jubatum Linnaeus [*Critesion jubatum* (Linnaeus) Nevski] [H; 2n = 14, 28, 42]. Occurs from upper Volga region to eastern Asia, introduced in North America. Traditionally placed in *Hordeum,* but moved to *Critesion* by Nevski (1934:721, 722), and treated in *Hordeum* subg. *Hordeastrum* (Doell) Rouy by Tzvelev (1976:281–284).

Caryopses: 3.5–4 mm long; oblanceolate or elliptic; compression dorsiventral, moderate to strong, dorsal face somewhat rounded; lateral ridges none; sulcus shallow, wide, slightly widened distally; corona ~0.5 mm long; apical hairs sparse to dense, length short to medium; embryo 1/4 as long as caryopsis (Figure 5*m–p*). (*Terrell s.n.,* 6 Jul 1977, Cache Co., Utah.)

Hordeum spontaneum K. Koch [*H. ithaburense* Boissier; *H. vulgare* subsp. *spontaneum* (K. Koch) Ascherson & Graebner] [I; 2n = 14]. Distributed from the Mediterranean region to central Asia. Placed in *Hordeum* subg. *Hordeum* by Tzvelev (1976:287).

Caryopses: 9–10 mm long; narrowly elliptic; compression dorsiventral, moderate, dorsal face flat or rounded; lateral ridges very small; sulcus shallow, narrow at base, widened to medium distally; corona 1–1.5 mm long, somewhat bilobed; apical hairs sparse, short; embryo 1/4 as long as caryopsis (Figure 6*a–d*). (**PI 466124,* Syria; *PI 466221,* Syria; *PI 466228,* Syria.)

Hordeum distichon Linnaeus [*Hordeum vulgare* subsp. *distichon* (Linnaeus) Koernicke] [I; 2n = 14]. Sometimes cultivated.

Caryopses: 8–8.5 mm long; elliptic; compression dorsiventral, slight, dorsal face rounded; lateral ridges none; sulcus shallow, narrow, widened distally to medium; corona 0.5–1 mm long; apical hairs sparse and short or lacking; embryo 1/3 as long as caryopsis (Figure 6*e–h*). (**CI 14311; CI 14310.*)

Hordeum vulgare Linnaeus [I; 2n = 14]. The type species is cultivated worldwide.

Caryopses: 7–10.5 mm long; elliptic or ovate; compression dorsiventral, slight or none (caryopsis round in transverse section); lateral ridges none; sulcus shallow, narrow, widened to medium at distal end; corona 0.5–1.5 mm long, conspicuous; apical hairs sparse and short, or lacking; embryo 1/4 as long as caryopsis (Figure 6*i–n*). (**CI 10640*-cv. Bonneville 70; **PI 328933,* cult. in Israel; **PI 356732,* cult. in Wales; *CI 14003.*)

Agropyron cristatum (Linnaeus) Gaertner sens. lat. [P; 2n = 14, 28, 42]. The type species is native in Europe and Asia, introduced in North America.

Caryopses: 3.5–4.5 mm long; oblong or lanceolate; compression dorsiventral, slight, dorsal face rounded; lateral ridges none; sulcus depth shallow to medium, width medium to narrow, slightly to somewhat widened distally; corona 0.5–1 mm long; apical hairs dense to sparse, short; embryo 1/4–1/5 as long as caryopsis (Figure 7*a–h*). (**PI 297869* (Figure 7*e–h*), Turkey; **PI 314596* (Figure 7*a–d*), Uzbekistan; *PI 330686,* Iran.)

Eremopyrum triticeum (Gaertner) Nevski (*Agropyron triticeum* Gaertner) [F; 2n = 14]. Native in southeast Europe and Asia Minor to central Asia, adventive in North America.

Caryopses: 2.5–4 mm long; lanceolate or ovate; compression dorsiventral, slight; dorsal face rounded; lateral ridges none; sulcus depth medium, narrow at base, widened to medium or wide distally; corona ~0.2–0.5 mm long, bilobed; apical hairs sparse, short; embryo 1/4 as long as caryopsis (Figure 7*i–q*). (*Terrell 4935,* Crook Co., Wyoming.)

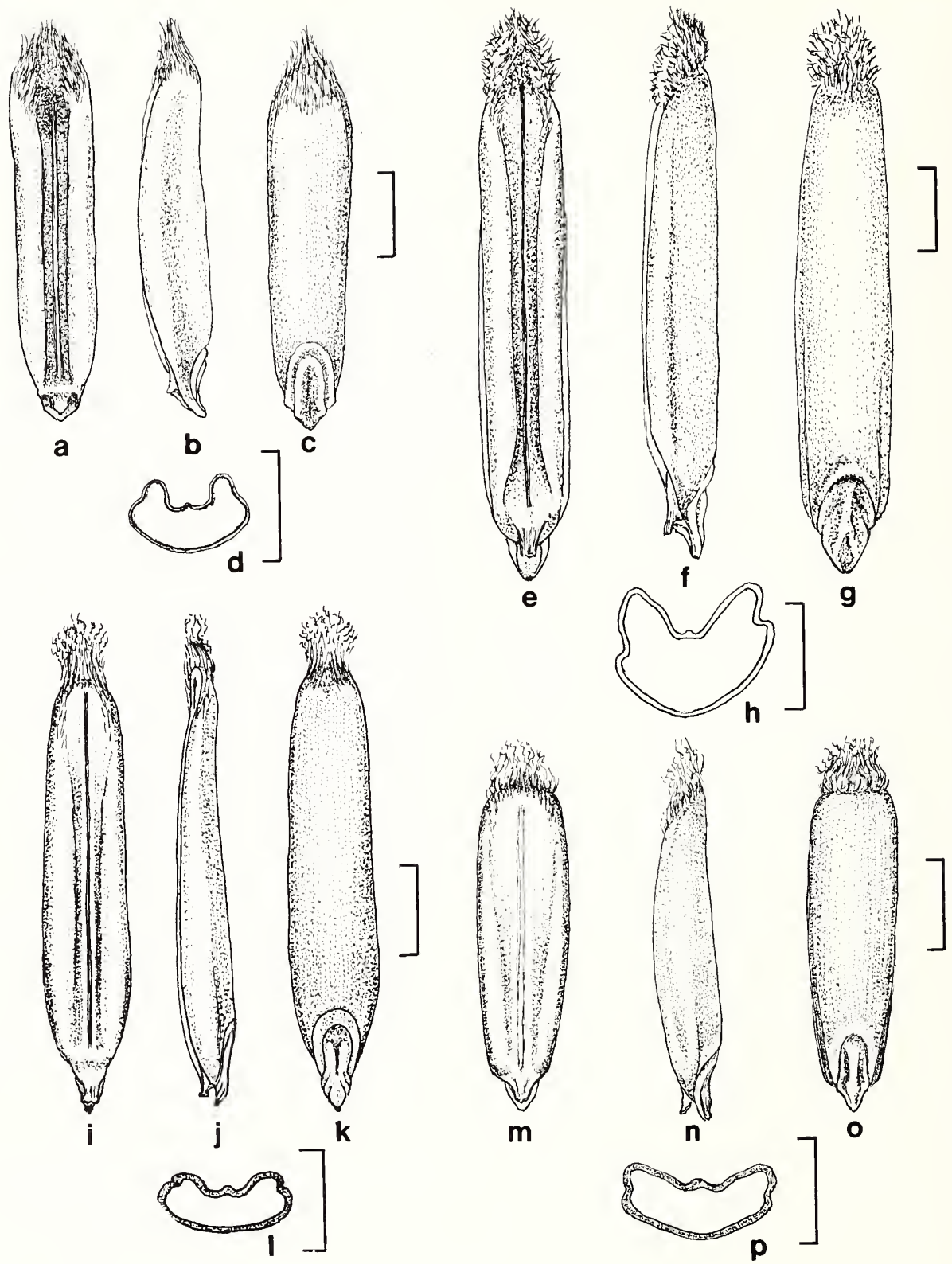

FIGURE 5.—Caryopsis of *Psathyrostachys juncea* (*a–d*); *Psathyrostachys fragilis* (*e–f*); *Hordeum bogdanii* (*i–l*); and *Hordeum jubatum* (*m–p*). Ventral views (*a,e,i,m*); lateral views (*b,f,j,n*); dorsal views (*c,g,k,o*); transverse sections (*d,h,l,p*). (All scales = 1 mm.)

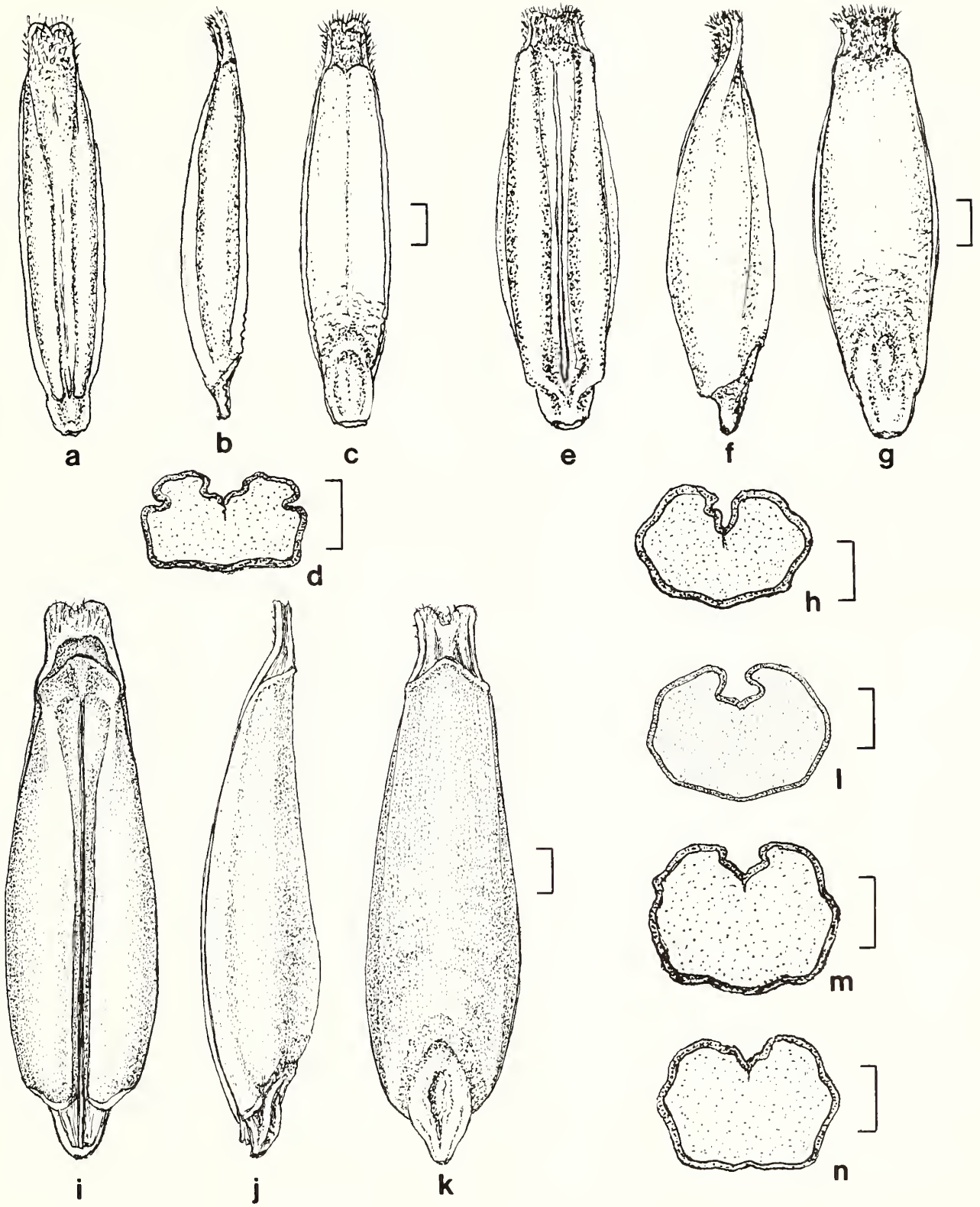

FIGURE 6.—Caryopsis of *Hordeum spontaneum* (*a–d*); *Hordeum distichon* (*e–h*), and *Hordeum vulgare* (*i–n*). Ventral views (*a,e,i*); lateral views (*b,f,j*); dorsal views (*c,g,k*); transverse sections (*d,h,l,m,n*). (All scales = 1 mm.)

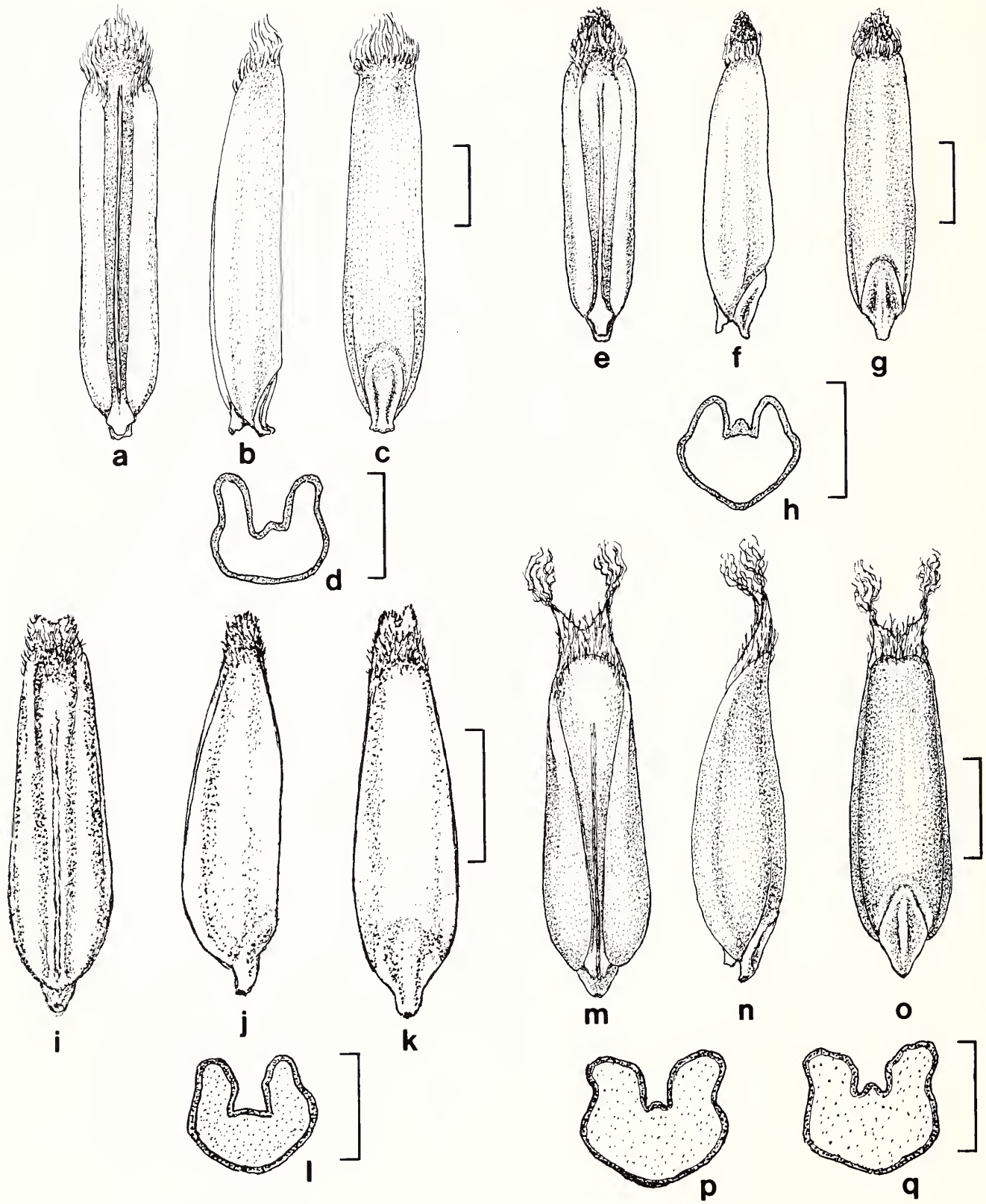

FIGURE 7.—Caryopsis of *Agropyron cristatum* (*a–h*) and *Eremopyrum triticeum* (*i–q*). Ventral views (*a,e,i,m*); lateral views (*b,f,j,n*); dorsal views (*c,g,k,o*); transverse sections (*d,h,l,p,q*). (All scales = 1 mm.)

Crithopsis delileana (Schultes) Roshevits [*Elymus delileanus* Schultes] [K; 2n = 14]. Ranges from the Mediterranean region to Iran (Bor, 1970:219; Melderis, 1980).

Caryopses: 4.5–5.5 mm long; lanceolate or narrowly elliptic; compression dorsiventral, strong, dorsal and ventral faces flattened; lateral ridges conspicuous; sulcus deep, width medium; corona 0.5–1 mm long; apical hairs sparse to dense, short; embryo 1/4 as long as caryopsis (Figure 8*a–d*). (**Bornmüller s.n.*, Nov. 1895, Palestine (US); *Barkley & Brahim M. 1337*, Iraq (US).)

Hordelymus europaeus (Linnaeus) C. Harz [*Elymus europaeus* Linnaeus; *Hordeum europaeum* (Linnaeus) Allioni; *Cuviera europaea* (Linnaeus) Koeler] [HT; 2n = 28]. Ranges from Europe to southwest Asia.

Caryopses: 7–7.5 mm long; narrowly lanceolate; compression dorsiventral, strong, dorsal face somewhat rounded; lateral ridges conspicuous; sulcus depth medium to deep, width medium; corona 0.5–1 mm long; apical hairs sparse to dense, length short to medium; embryo 1/5–1/6 as long as caryopsis (Figure 8*e–h*). (*E. Nelmes 151*, England (US).)

Taeniatherum caput-medusae (Linnaeus) Nevski, sens. lat. [*Elymus caput-medusae* Linnaeus; including *T. asperum* (Simonkai) Nevski and *T. crinitum* (Schreber) Nevski] [T; 2n = 14]. Occurs in Europe and North Africa and ranges to central Asia and the Himalayas.

Caryopses: 5.5–9 mm long; narrowly lanceolate; compression dorsiventral, strong, dorsal face rounded; lateral ridges conspicuous; sulcus medium to deep, narrow to medium, slightly widened distally; corona 0.5 mm long; apical hairs sparse to dense, length short to medium; embryo about 1/5 as long as caryopsis (Figure 8*i–m*). (**BN 20815-70*, France, SCS, USDA; *Vasey 3076*, Washington state (US).)

Aegilops cylindrica Host [*Triticum cylindricum* (Host) Cesati] [CD; 2n = 28]. Ranges from central Europe and the Mediterranean region to central Asia, adventive in North America.

Caryopses: 5.5–8.5 mm long; lanceolate or narrowly elliptic; compression dorsiventral, moderate, dorsal face somewhat rounded, ventral face flattened; lateral ridges none; sulcus shallow, narrow and almost closed, sometimes widened at distal end; corona ~1 mm long, somewhat like a cap; apical hairs dense, length medium; embryo 1/3–1/5 as long as caryopsis (Figure 9*a–p*). (*Terrell 4841*, Weber Co., Utah.)

Comment: Each spikelet has two fertile florets of which both or one may produce caryopses. If two are produced, they differ in size and sometimes slightly in shape. Two pairs of spikelets are drawn, each spikelet with 2 caryopses to show the variation.

Aegilops triuncialis Linnaeus [*Triticum triunciale* (Linnaeus) Raspail] [CU; 2n = 28]. Ranges from the Mediterranean region to central Asia.

Caryopses: 6.5–8.5 mm long; lanceolate or narrowly elliptic; compression dorsiventral, moderate, dorsal face somewhat rounded, ventral face flattened or slightly rounded or concave; lateral ridges none; sulcus shallow to medium, closed and with a small opening adjacent to hilum; corona 0.5–1.5 mm long, somewhat cap-like; apical hairs dense, length short to medium; embryo 1/3–1/4 as long as caryopsis (Figure 10*a–h*). (*PI 276991*, Afghanistan.)

Amblyopyrum muticum (Boissier) Eig [*Aegilops mutica* Boissier; *A. tripsacoides* Jaubert & Spach, *Triticum tripsacoides* (Jaubert & Spach) Bowden] [Z; 2n = 14]. Native to Asia Minor and Caucasus.

Caryopses: 3.5–4 mm long; elliptic or oblong; compression dorsiventral, moderate or strong, dorsal face rounded, ventral face flattened or broadly V-shape; lateral ridges none; sulcus shallow, width medium; corona 0.5–1 mm long, somewhat cap-like; apical hairs sparse to dense, short; embryo 1/3 as long as caryopsis (Figure 10*i–n*). (**Bot. Exped. Kyoto Univ. 7-1-4-D, 7-1-4-C*, Turkey (US).)

Triticum monococcum Linnaeus [*Crithodium monococcum* (Linnaeus) Löve] [A; 2n = 14]. Native in Europe and the Mediterranean region to Caucasus and Iran.

Caryopses: 7.5–9.5 mm long; ovate or elliptic; compression none or slight, caryopses circular in transverse section or ventral face slightly compressed; lateral ridges none; sulcus depth medium to deep, sulcus closed, with a small rounded opening adjacent to hilum; corona 1–2 mm long, cap-like; apical hairs dense to sparse, length short to long; embryo 2/5–1/3 as long as caryopsis (Figure 11*a–d*). (**PI 94738*, cultivated, St. Petersburg, Russian Federation; *PI 168805*, cult. in Kansas.)

Triticum dicoccon Schrank sens. lat. (sens. Tzvelev, 1976:237, 238) [AB; 2n = 28]. Native to the Mediterranean region and southwest Asia.

Caryopses: 9–11 mm long; ovate or elliptic; compression none, caryopses circular in transverse section or irregularly compressed; lateral ridges none; sulcus medium to deep, closed, with a small rounded opening adjacent to hilum; corona 1–2.5 mm long, cap-like; apical hairs dense, length medium to long; embryo 1/3–1/4 as long as caryopsis (Figure 11*e–h*). (**PI 94664* and *PI 94613*, cultivated in Saudi Arabia.)

Triticum aestivum Linnaeus [ABD; 2n = 42]. Bread wheat, the type species, is cultivated worldwide.

Caryopses: 5.5–7.2 mm long; ovate, broadly elliptic, or broadly oblong; compression none or slight, caryopsis

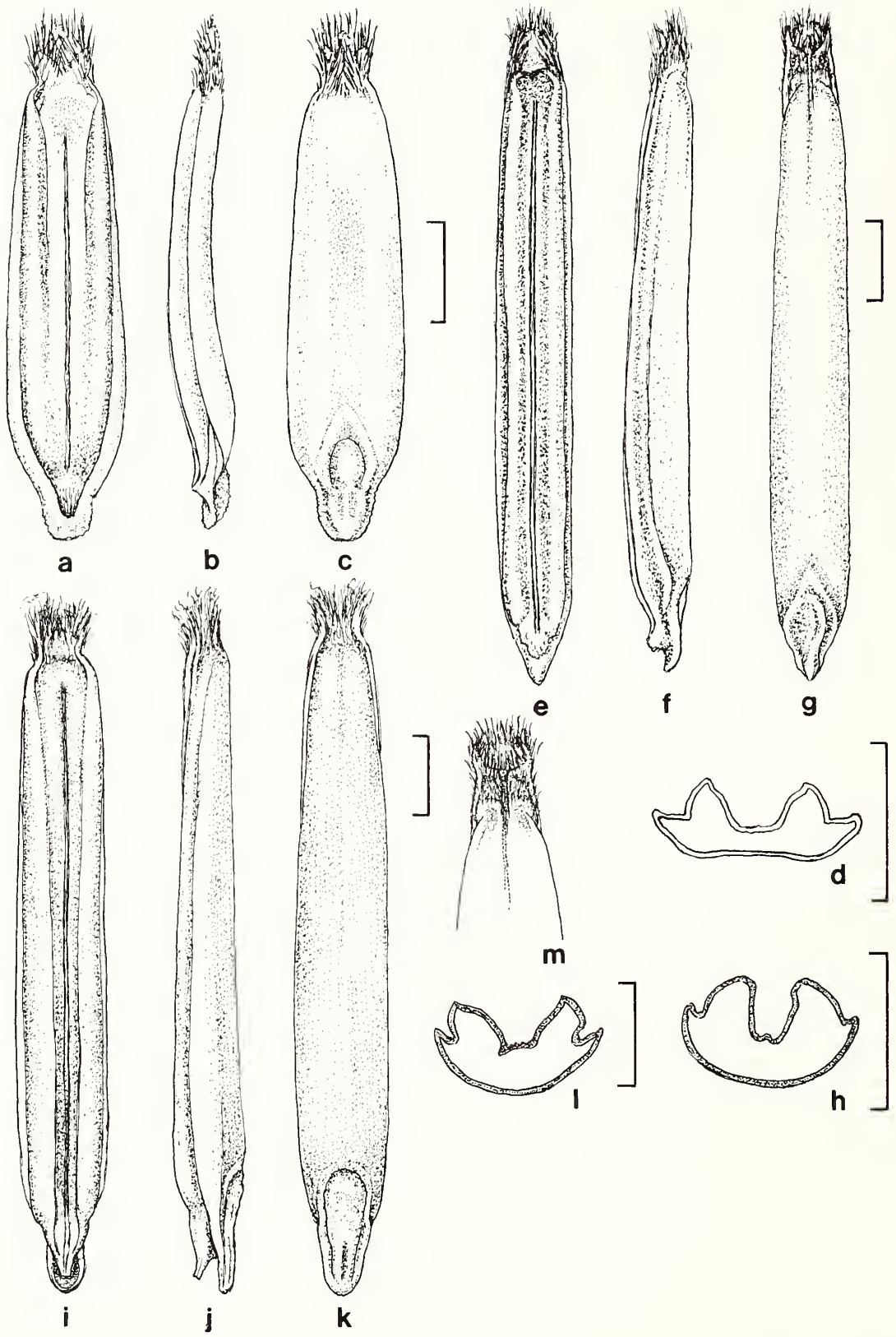

FIGURE 8.—Caryopsis of *Crithopsis delileana* (*a–d*); *Hordelymus europaeus* (*e–h*); and *Taeniatherum caput-medusae* (*i–m*). Ventral views (*a,e,i,m*); lateral views (*b,f,j*); dorsal views (*c,g,k*). (All scales = 1 mm.)

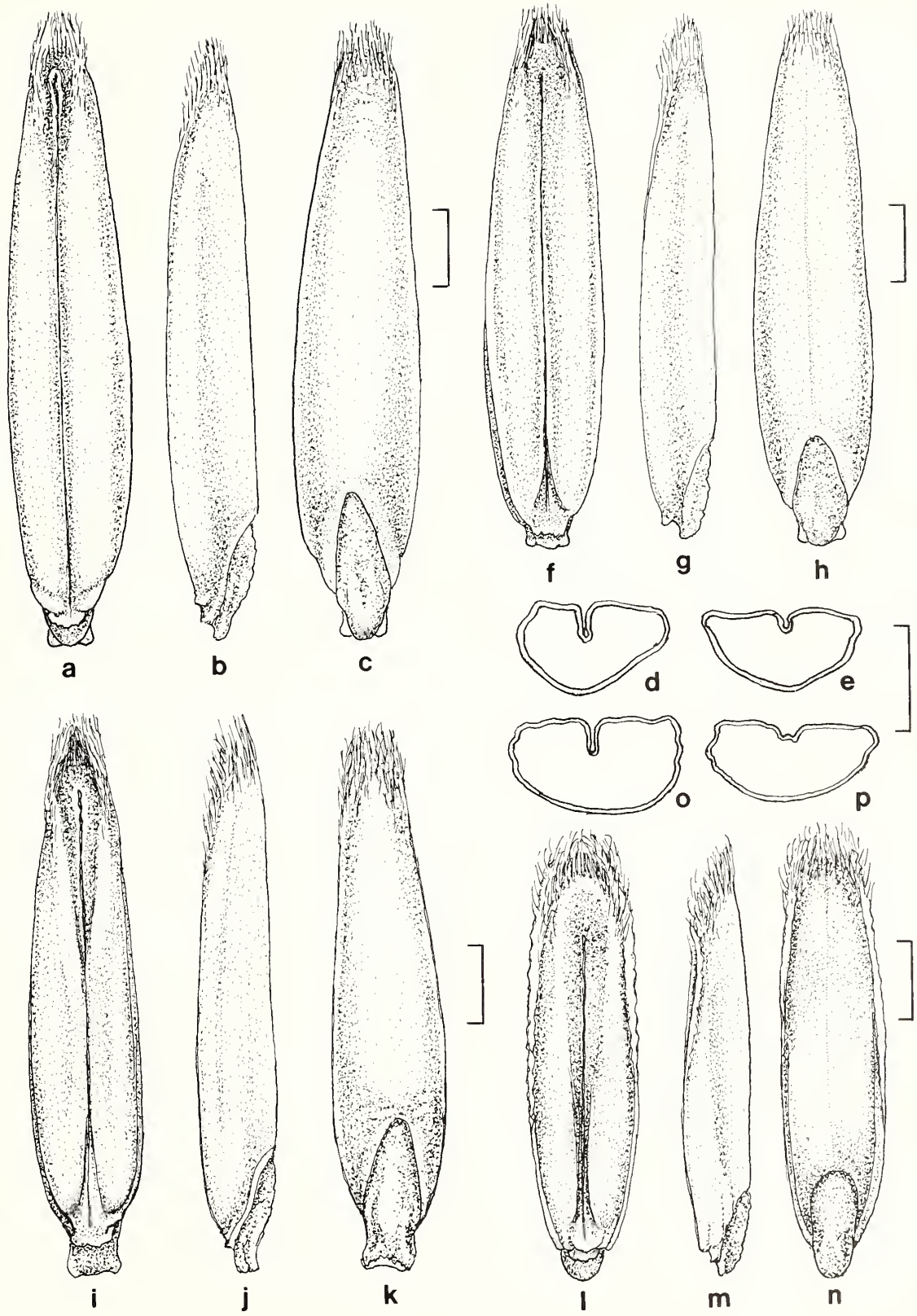

FIGURE 9.—Caryopsis of *Aegilops cylindrica* (*a–p*). Ventral views (*a,f,i,l*); lateral views (*b,g,j,m*); dorsal views (*c,h,k,n*); transverse sections (*d,e,o,p*). (All scales = 1 mm.)

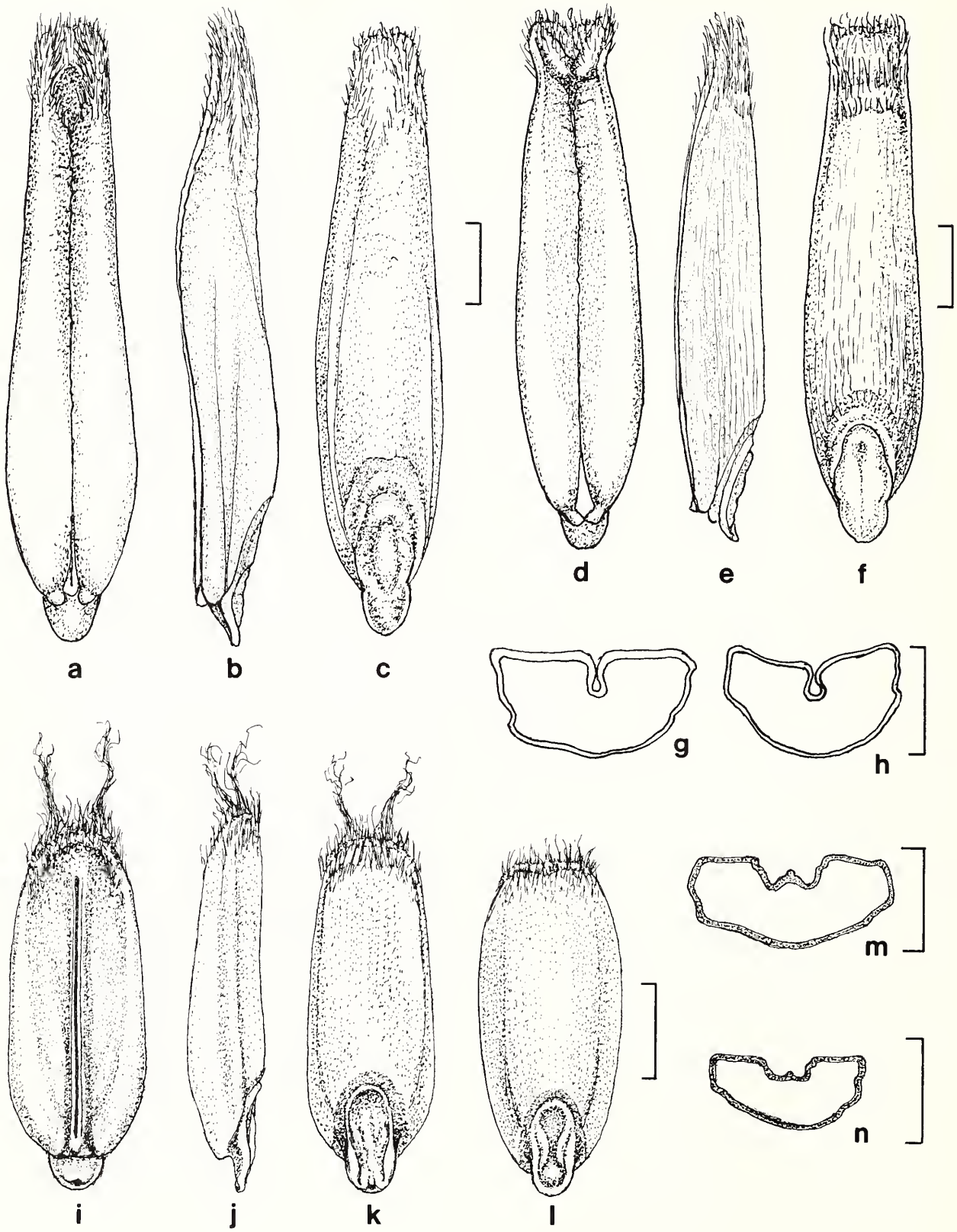

FIGURE 10.—Caryopsis of *Aegilops triuncialis* (*a–h*) and *Amblyopyrum muticum* (*i–n*). Ventral views (*a,d,i*); lateral views (*b,e,j*); dorsal views (*c,f,k,l*); transverse sections (*g,h,m,n*). (All scales = 1 mm.)

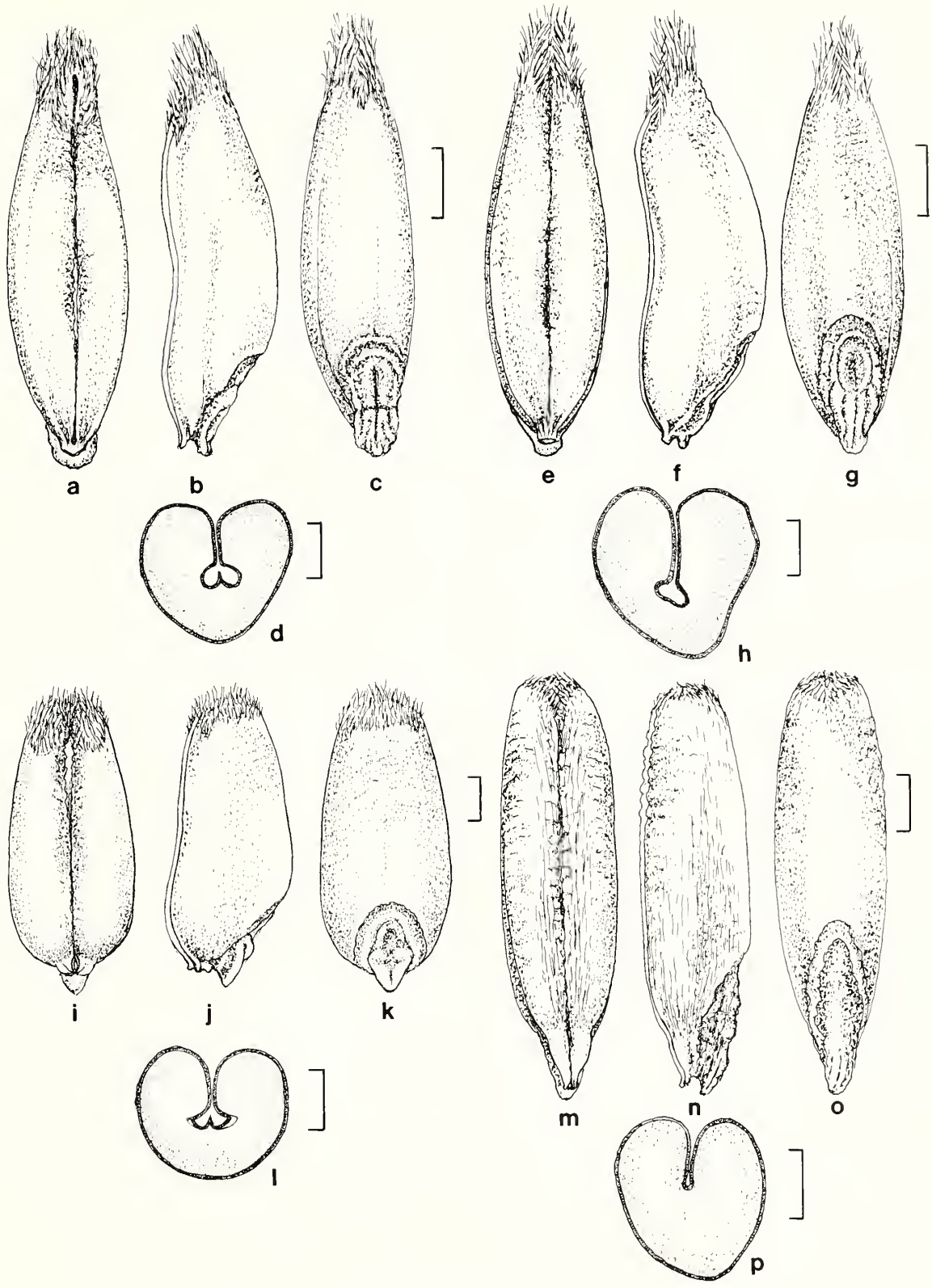

FIGURE 11.—Caryopsis of *Triticum monococcum* (*a–d*); *Triticum dicoccon* (*e–h*); *Triticum aestivum* (*i–l*); and *Secale cereale* (*m–p*). Ventral views (*a,e,i,m*); lateral views (*b,f,j,n*); dorsal views (*c,g,k,o*); transverse sections (*d,h,l,p*). (All scales = 1 mm.)

circular in transverse section or slightly compressed ventrally; lateral ridges none; sulcus deep to medium, very narrow or closed, with small rounded space adjacent to hilum; corona 0.5–1.5 mm long, cap-like; apical hairs dense, short to long; embryo 1/3–1/4 as long as caryopsis (Figure 11*i–l*). (**CI 13448*-cv. Gaines; *CI 17745*-cv. Dirkwin.)

Comment: Descriptions from Bayles and Clark (1954) were added to this, but there is much more variation not included here.

Secale cereale Linnaeus [R; 2n = 14]. The type species, rye, is cultivated worldwide.

Caryopses: 6–10 mm long; elliptic or oblong; compression none, caryopses circular in transverse section; lateral ridges none; sulcus depth medium, closed, with a very small opening adjacent to hilum; corona 0.5 mm long, cap-like; apical hairs sparse and short or absent; embryo 2/5–1/3 as long as caryopsis (Figure 11*m–p*). (*PI 535198*-cv. Weser, cult. in Canada.)

Dasypyrum villosum (Linnaeus) Candargy [*Haynaldia villosa* (Linnaeus) Schur] [V; 2n = 14]. This species occurs in central Europe and the Mediterranean region to southwest Asia.

Caryopses: 3.8–7 mm long; oblong or elliptic, variable in shape; compression lateral, slightly to strongly compressed; lateral ridges none; sulcus shallow, medium or narrow to closed; corona 0.5–1.5 mm long, forming an angled cap, the two style bases sometimes persistent; apical hairs sparse and short or absent; embryo 1/4 as long as caryopsis (Figure 12*a–d*). (**C. Chapman s.n.*, Jul 1984, Rome, Italy, via USDA; *PI 368886*, Turkey.)

Heteranthelium piliferum (Banks & Solander) Hochstetter [Q; 2n = 14]. Occurs in the eastern Mediterranean region and central Asia.

Caryopses: 5–7.5 mm long; oblong in dorsal view, elliptic in lateral view; compression lateral, moderate, dorsal face rounded, ventral face somewhat flattened or broadly V-shape; lateral ridges none; sulcus medium to deep, very narrow or closed, with small rounded opening adjacent to hilum; corona 1–1.5 mm long, cap-like; apex of caryopsis obtuse or with two acuminate style bases; apical hairs sparse to dense, short, or absent; embryo 1/3–1/4 as long as caryopsis (Figure 12*e–i*). (**Bot. Exped. Kyoto Univ. 5-28-1-C*, Iraq (US); *Bornmüller 1678*, Syria (US); *PI 401351*, Iran.)

Comment: Caryopses appear to be somewhat heteromorphic.

Henrardia persica (Boissier) C.E. Hubbard [O; 2n = 14]. This type species occurs in the eastern Mediterranean region to central Asia.

Caryopses: 4.8–6.2 mm long; lanceolate or oblong; compression dorsiventral, moderate to strong, dorsal face flattened or slightly concave, ventral face concave to rounded; lateral ridges none; sulcus very shallow, narrow to medium; corona 0.2–0.5 mm long, cap-like?; apical hairs sparse to dense, short; embryo 1/3 as long as caryopsis (Figure 12*j–m*). (**Mokeeva 527*, Tian-schan, central Asia (K); *PI 401347-9*, Iran.)

Brachypodium pinnatum (Linnaeus) P. Beauvois [2n = 28]. The type species is native in Europe, southwest Asia, and northwest Africa.

Caryopses: 6–7 mm long; lanceolate or oblong; compression dorsiventral, moderate, dorsal face rounded or somewhat flattened; lateral ridges none; sulcus depth medium, width wide; corona 0.5 mm long; apical hairs dense, short; embryo 1/5–1/6 as long as caryopsis (Figure 12*n–q*). (*PI 251803*, Italy.)

Discussion

The characters showing significant differences among genera have been tabulated for comparison (Table 2). The shared characteristics of the caryopses have lead us to recognize the following three groups: elymoid, triticinoid, and henrardioid. A fourth entity is *Brachypodium*, which according to our data remains controversial. The previously recognized limits of the subtribe Triticinae are indistinct and inconsistent as used by various authors (e.g., Tzvelev, 1976), and they do not coincide with the limits we recognize on the basis of caryopsis structure.

ELYMOID GROUP.—The elymoid group examined in this study includes *Elymus, Elytrigia, Leymus, Psathyrostachys, Agropyron, Eremopyrum, Hordeum, Crithopsis, Hordelymus,* and *Taeniatherum.*

The elymoid caryopsis characters are as follows: caryopses 2.5–11 mm long, not heteromorphic, although sometimes differing slightly in size within one spikelet; caryopses usually oblong, oblanceolate, lanceolate, or elliptic; compression dorsiventral (slight–) moderate to strong, flattened more on ventral face than on dorsal; lateral ridges absent or rudimentary, large in *Crithopsis, Taeniatherum,* and *Hordelymus;* sulcus depth shallow to medium, width (narrow–) medium to wide, often widened distally; corona a thin whitish or yellowish flattened apical membrane, usually bearing apical hairs; apical hairs usually dense (–sparse), (short–) medium to long; embryo (1/3–) 1/4–1/5 (–1/6) as long as caryopsis.

Two of the species included in *Elymus* traditionally were placed in *Hystrix* and *Sitanion: E. hystrix* (*Hystrix patula*) and *E. elymoides* (*Sitanion hystrix*). *Sitanion* was treated in a traditional sense by Wilson (1963). Church (1967a,b) advocated the union of *Hystrix* and *Elymus* after finding natural hybrids between them. Dewey (1982, 1984:246–250) and Löve (1984:447) united both *Hystrix* and *Sitanion* in *Elymus*, Löve recognizing them as sections. Clayton and Renvoize

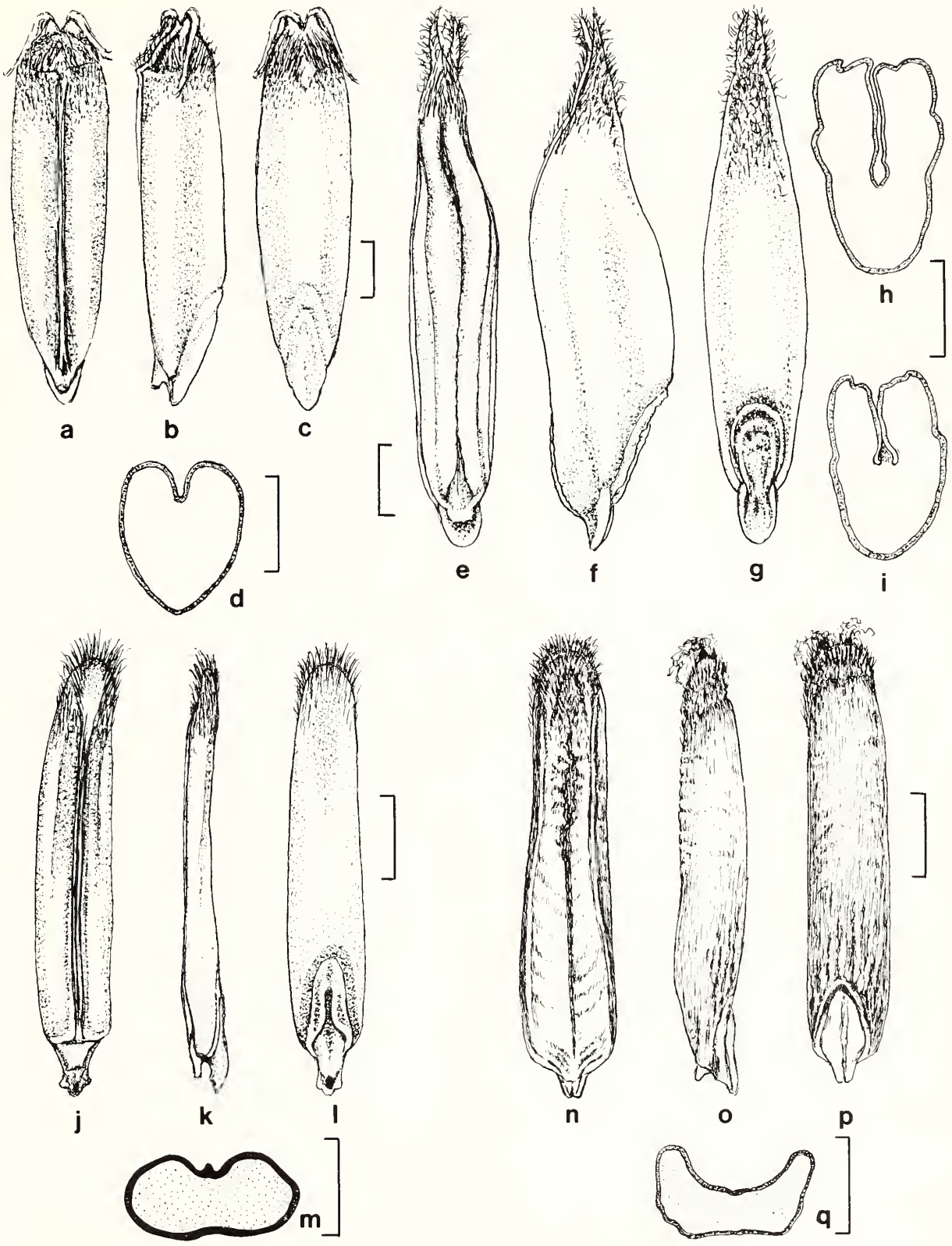

FIGURE 12.—Caryopsis of *Dasypyrum villosum* (*a–d*), *Heteranthelium piliferum* (*e–i*), *Henrardia persica* (*j–m*), and *Brachypodium pinnatum* (*n–q*). Ventral views (*a,e,j,n*); lateral views (*b,f,k,o*); dorsal views (*c,g,l,p*); transverse sections (*d,h,i,m,q*). (All scales = 1 mm.)

TABLE 2.—Morphological variation in selected characters. (Abbreviations as follows: abs = absent; cap = cap-like; clos = closed; dv = dorsiventral; dvvf = dorsiventral with ventral face flattened; n. = narrowly; ell = elliptic; lat = lateral; lanc = lanceolate; med = medium; mod = moderate; narr = narrow; oblanc = oblanceolate; rud = rudimentary; shal = shallow; slt = slight; str = strong; vert = vertical.)

Species	Shape	Compression		Sulcus		Ridge	Corona
		Extent	Depth	Depth	Width		
Elymus sibiricus	oblanc/oblong	dv	mod	shal	med/wide	abs	vert
E. dahuricus	"	"	"	"	"	"	"
E. caninus	"	"	"	"	"	"	"
E. hystrix	"	"	"	"	"	"	"
E. elymoides	"	"	"	shal/med	"	"	"
E. distichus	lanc/n. ell	"	mod/str	med/deep	wide	"	"
Elytrigia repens	oblong	"	slt	shal/med	med	"	"
E. elongata	"	"	mod	shal	med/wide	"	"
E. spicata	oblong/n. ell	"	mod/str	deep	wide	"	"
Leymus arenarius	oblanc/oblong	"	"	med	"	"	"
L. angustus	oblong/lanc	"	mod	med	med/wide	rud/abs	"
L. alaicus	oblong	"	"	shal/med	med/wide	rud	"
Psathyrostachys juncea	oblanc/oblong	"	"	med	med/wide	rud/abs	"
P. fragilis	oblong	"	"	"	"	rud	"
Hordeum bogdanii	oblong/lanc	"	mod/str	shal/med	med	abs	"
H. jubatum	oblanc/ell	"	"	shal	wide	"	"
H. spontaneum	n. ell	"	mod	"	narr/med	small	"
H. distichon	ell	"	slt	"	"	abs	"
H. vulgare	ell/ovate	"	slt/none	"	"	"	"
Agropyron cristatum	oblong/lanc	"	slt	shal/med	narr/med	"	"
Eremopyron triticeum	lanc/ovate	"	"	med	narr/wide	"	"
Crithopsis delileana	lanc/n. ell	"	str	deep	med	large	"
Hordelymus europaeus	n. lanc	"	"	med/deep	"	"	"
Taeniatherum caput-medusae	"	"	"	"	narr/med	"	"
Aegilops cylindrica	lanc/n. ell	dvvf	mod	shal	narr/clos	abs	cap
A. triuncialis	"	"	"	shal/med	clos	"	"
Amblyopyron muticum	ell/oblong	"	mod/str	shal	med	"	"
Triticum monococcum	ovate/ell	none/slt	–	med/deep	clos	"	"
T. dicoccon	"	none	–	"	"	"	"
T. aestivum	"	none/slt	–	"	"	"	"
Secale cereale	oblong/ell	none	–	med	"	"	"
Dasypyron villosum	"	lat	slt/str	shal	med/clos	"	"
Heteranthelium piliferum	"	"	mod	med/deep	clos	"	"
Henrardia persica	lanc/oblong	dv	mod/str	shal	narr/med	"	cap?
Brachypodium pinnatum	"	"	"	med	wide	"	vert

(1986:151, 152) recognized *Hystrix* and *Sitanion* as good genera and included *Cockaynea* Zotov from New Zealand in *Hystrix*. Differences among the caryopses of *E. hystrix, E. elymoides,* and the other *Elymus* species with an SH genome are minor, although *E. elymoides* and *E. hystrix* have distinct morphological differences in other characters, such as inflorescence structure and glume shape and length. In view of the latter differences, we believe that *Hystrix* and *Sitanion,* although obviously closely related to *Elymus,* deserve further study before being subsumed in *Elymus*.

There are other minor differences among *Elymus* species having the SH genome. *Elymus dahuricus* and *E. caninus* have caryopses in which the sulcus widens distally (Figure 2*e,i*), whereas in other species of *Elymus* the sulcus is equally wide near the base and apex of the caryopsis. This state is not peculiar to genera with the SH genome as it also is found in *Elytrigia* and *Leymus*.

Elymus distichus, traditionally in *Agropyron,* was placed in *Elymus* sect. *Junceae* (Prat) Melderis by Melderis (1978b) and in *Thinopyrum* by Löve (1984). It has the J or JE genome. The caryopses are unusually large and strongly compressed for *Elymus* and are distinctive in having a large, broad, somewhat auriculate corona sparsely beset with short hairs (Figure 3*e*). This species differs from other species of *Elymus* and deserves further study along with other members of sect. *Junceae*.

The three species of *Elytrigia* examined have an SX genome (*E. repens*), an E genome (*E. elongata*), and an S genome (*E. spicata*); however, the species do not differ in any distinctive characteristics. The caryopses of *Elytrigia repens* (Figure 3*i–l*) are less compressed and have a narrower sulcus than those of *E.*

spicata (Figure 4*a–d*). The caryopses of *Elytrigia elongata* (Figure 3*m–p*) are similar to the other species of *Elymus* examined.

Psathyrostachys fragilis is morphologically distinct from the other species of the genus (Baden, 1991) in having readily disarticulating spikelets with very long awns. The examined species of *Psathyrostachys* and *Leymus* have similar caryopses (Figures 4*e–l*, 5*a–f*), spikelets, and florets (e.g., compare spikelets and florets of *Leymus cinereus* (Scribner & Merrill) Löve and *Psathyrostachys junceus*). Their genomes also indicate a close relationship, as *Psathyrostachys* contains the N and *Leymus* the JN genomes.

In summary, caryopses of the 14 examined species of *Elymus, Elytrigia, Leymus,* and *Psathyrostachys* generally are similar in morphology. There does not seem to be any particular set of character states that occur in one genome or genus and not in others; e.g., caryopses of *Elymus caninus, Elytrigia elongata,* and *Leymus alaicus* subsp. *karataviensis* are very similar. *Elytrigia repens* and *Psathyrostachys fragilis* are somewhat similar, as are *Elymus sibiricus* and *Leymus arenarius*. The caryopses of *Leymus* and *Psathyrostachys* are similar in all the species sampled. If there are character states hidden within the caryopsis that are characteristic or predominant within any particular genome, a much larger sampling of a range of species would be necessary to reveal them. We conclude that similarities among caryopses of the four genera are more significant than the minor differences found in this study. Based on caryopsis morphology our results suggest that *Elytrigia, Leymus,* and *Psathyrostachys* might be included in a broad genus *Elymus,* a course espoused by Estes and Tyrl (1982).

Hordeum, with its characteristic triads or groups of three spikelets, is a fully distinct genus. Bothmer et al. (1984) recognized four sections in *Hordeum*. These are represented in the present study: sect. *Hordeum* by *H. spontaneum, H. distichon,* and *H. vulgare;* sect. *Anisolepis* by *H. pusillum* (SEM photo only); sect. *Critesion* by *H. jubatum;* and sect. *Stenostachys* by *H. bogdanii*. Löve (1984:436–441) placed the latter two species in a separate genus, *Critesion*. Caryopses of *Hordeum bogdanii* and *H. jubatum* (Figure 5*i–p*) are similar to each other and to species of *Elymus* (Figures 2*a–q*, 3*a–h*).

Hordeum spontaneum, H. distichon, and *H. vulgare* (Figure 6*a–n*) have similar caryopses, but differ from *H. bogdanii* and *H. jubatum* (Figure 5*i–p*); consequently, there appears to be two groups based on the caryopses characters. The caryopsis evidence seems to suggest that *Hordeum* sect. *Hordeum* is a distinct entity, whether section, subgenus, or genus (true *Hordeum*), but certainly caryopses of additional species need to be studied. We are unsure as to the distinctiveness of *Critesion* from *Hordeum,* as our limited sample does not allow speculation.

The crested wheatgrass complex is morphologically distinct from the traditional *Agropyron* species now shifted to *Elymus*. The caryopsis of *Agropyron cristatum* (Figure 7*a–h*) differs from the illustrated species of *Elymus* by having only slight dorsiventral compression, a deeper and narrow or medium-wide sulcus, and shorter apical hairs. Although the systematic relationships of *Eremopyrum* (Frederiksen, 1991b) have been controversial, Bowden (1962) and Clayton and Renvoize (1986:155) suggested that the genus is closely related to the *Agropyron cristatum* group. We agree with this assessment because the inflorescence, spikelets, florets, and caryopses resemble those of *A. cristatum* (Figure 7*i–q*).

Crithopsis and *Hordelymus* are monotypic genera with caryopses having rather strong ventral compression, a deep and rather wide sulcus, conspicuous lateral ridges, and similar coronas (Figure 8*a–h*). The caryopses of *Taeniatherum* are less strongly compressed, have a medium-deep and medium-wide sulcus, and conspicuous lateral ridges (Figure 8*i–m*). These three genera possess similar caryopses and seem to be somewhat distinct from the other elymoid genera.

TRITICINOID GROUP.—The triticinoid group includes *Aegilops, Amblyopyrum, Triticum, Secale, Dasypyrum,* and *Heteranthelium*.

The triticinoid caryopses characters are as follows: caryopses 4–11 mm long; lanceolate or oblong to elliptic or ovate; compression none, or flattened dorsiventrally only on the ventral side, or slightly to strongly flattened laterally; sulcus depth varying from shallow to deep; sulcus width very narrow or closed; corona cap-like; apical hairs dense or often sparse, length short or medium, hairs sometimes lacking in *Dasypyrum, Heteranthelium,* and *Secale;* embryo ($^2/_5$–) $^1/_3$–$^1/_4$ (–$^1/_5$) as long as caryopsis; caryopses slightly or somewhat heteromorphic (differing in size and shape in florets from the same spikelet) in *Aegilops, Dasypyrum,* and *Heteranthelium*.

Aegilops and *Triticum* are sometimes united (e.g., Bowden, 1959), maintained as distinct (e.g., Tutin and Humphries, 1980), or divided into several genera (Löve, 1984:491–498). The caryopses of *Aegilops cylindrica* and *A. triuncialis* resemble one another by having ventrally flattened caryopses with shallow sulci (Figures 9, 10*a–h*). The caryopses of *Triticum* conspicuously differ from these species of *Aegilops* by being ventrally rounded with medium to deep sulci with a small open area adjacent to the hilum (Figure 11*a–l*). However, the caryopses of *Aegilops ovata* Linnaeus and *A. umbellulata* Zhukovsky (not illustrated) show resemblances to wheat. On account of the few species studied, we cannot provide any definite conclusions on the degree of interrelationships between *Aegilops* and *Triticum*.

Aegilops cylindrica, A. triuncialis, and other species in the genus usually have two fertile florets per spikelet. The two resulting caryopses present in the spikelet differ in size and to a lesser degree in shape (Figures 9*a–p*, 10*a–h*). Caryopsis differences within a spikelet also were seen (not illustrated) in *A. squarrosa* Linnaeus (collection USDA CI 8) where one floret contained a caryopsis 5.8 mm long × 3.2 mm wide, whereas the other floret bore a caryopsis 5.2 mm × 3.2 mm. Another spikelet contained caryopses 5.6 mm long × 3.1 mm

wide and 5.0 mm long × 3.0 mm wide. This heteromorphism or heterocarpism in the two caryopses of one spikelet is perhaps uncommon in grasses or at least inadequately documented, although any grass species with several florets per spikelet may have caryopses that differ slightly in size within the same spikelet (e.g., *Lolium* and *Festuca*).

Amblyopyrum muticum was treated as distinct from *Aegilops* by several authors (e.g., Bor, 1968:224–226; Tzvelev, 1976:219, 220). Its caryopses differ somewhat from the two species of *Aegilops* illustrated here in shape and in having a wider sulcus (Figure 10*i–n*).

Triticum monococcum and *T. dicoccon*, wild relatives of wheat, have caryopses that are almost identical (Figure 11*a–h*). Their caryopses are not compressed but are rounded in transverse section and have a deep, closed sulcus. *Triticum aestivum* (wheat) has shorter, broader, and more ovate caryopses (Figure 11*i–l*). *Triticum aestivum* and *Secale cereale* (rye) caryopses are basically similar in transverse section and differ mainly in size and shape (Figure 11*m–p*). The similarity in caryopsis morphology between *Triticum* and *Secale* is consistent with their known genetic compatibilities in crossing successfully to produce the hybrid triticale.

Dasypyrum villosum (Figure 12*a–d*) is distinctly set off from *Triticum* (Figure 11*a–l*) by having slightly to strongly compressed caryopses with a corona forming an angled cap usually with persistent style bases. However, the characteristics of the inflorescence, spikelet, and to some extent the caryopsis align *Dasypyrum* with the triticinoid group. It also is known to hybridize with *Triticum* (Frederiksen, 1991a). *Heteranthelium piliferum* (Figure 12*e–i*) has certain distinctive characters, such as a strongly laterally compressed caryopsis with a rather deep sulcus and apical acuminate style bases, but the caryopsis has obvious resemblances to *Triticum* and *Dasypyrum*.

HENRARDIOID GROUP.—The henrardioid group includes only *Henrardia*, an anomalous genus whose systematic position has been controversial. The two species of *Henrardia* formerly were placed in *Pholiurus* or *Lepturus* (now in tribe Hainardieae according to Tutin, 1980) until Hubbard (1946) created the new genus *Henrardia* and placed it in the Triticeae (as Hordeae) on the basis of lemma nervation, lodicules, ovaries, and caryopses. The genus sometimes has been placed in its own subtribe, Henrardiinae Hubbard in Hook.

Caryopses of *Henrardia persica* resemble other Triticeae in having a linear hilum, a corona with apical hairs, and a sulcus (Figure 12*j–m*). They are like the elymoid genera in having a generally lanceolate or oblong shape and rather strong dorsiventral compression (Figures 2, 3*a–h*). However, the caryopses are unusual in having a particular combination of characteristics not found in any other members of the Triticeae. The dorsal and ventral faces of the caryopses are equally compressed with a very shallow, narrow sulcus, its margins low and rounded (unlike the elymoid species), and a small corona with apical hairs usually sparse and short (Figure 12*j–m*). Clayton and Renvoize (1986:158) noted that *Henrardia* although seemingly aberrant is not far removed from *Aegilops* sect. *Vertebrata* (*A. ventricosa* Tausch). Our sampling of *Aegilops* species is insufficient to test this opinion. *Henrardia* appears to belong in the Triticeae and its caryopsis morphology suggests that it represents a distinct subtribe.

BRACHYPODIUM GROUP.—*Brachypodium* is a genus of controversial alliances, placed in the Triticeae by Clayton and Renvoize (1986:148–150) but most often treated in its own tribe, Brachypodieae Hackel, or considered close to the Bromeae (Macfarlane and Watson, 1982). The caryopses of *Brachypodium pinnatum* (Figure 12*n–q*) are somewhat similar to elymoid species (Figures 2, 3*a–h*) in shape and sulcus morphology. This species has a chromosome number of 2n = 28, which agrees with the basic number of 7 for the tribe. Other species of *Brachypodium* differ in chromosome number and have been found to possess base numbers of 5 and 9 (2n = 38), thus suggesting that *Brachypodium* as traditionally constituted is heterogeneous. We examined caryopses of two other species (not illustrated), *B. sylvaticum* (Hudson) P. Beauvois [*Brevipodium sylvaticum* (Hudson) A. & D. Löve] with x = 7, 9 (Veldkamp and van Scheindelen, 1989) and *B. distachyon* (Linnaeus) P. Beauvois [*Trachynia distachya* (Linnaeus) Link] with 2n = 28 or 30. Both of these species have caryopses generally similar to those of *B. pinnatum*. The caryopses of *Brachypodium* also resemble those of *Bromus* (Bromeae). Based on chloroplast DNA restriction site variation within the Pooideae, Soreng et al. (1990) found that *Brachypodium pinnatum, Bromus inermis* Leysser, and *Hordeum vulgare* always formed a clade representing the supertribe Triticodae. Based on the phytochemical characters Veldkamp and van Scheindelen (1989) stated that *Brachypodium* differs from the Triticeae and Bromeae. We are uncertain whether *Brachypodium* belongs in this tribe, considering the conflicting evidence and its similarity in caryopsis structure to *Bromus* and the Bromeae.

CARYOPSES CHARACTERISTICS OF THE TRITICEAE.—In addition to the characters we employed to analyze triticoid variation, there are other characters that are characteristic for the Triticeae as a whole that sometimes distinguish this tribe from certain other tribes (Terrell, unpublished). We take this opportunity to summarize these here and also to include the embryo characters studied intensively by Reeder (1957). The caryopses of the Triticeae have the following principal tribal diagnostic characteristics: (1) caryopses relatively large, 2.5–11 mm long in taxa studied; (2) compression in the elymoid and henrardioid genera and *Brachypodium* usually moderately to strongly dorsiventral, sometimes unequal on dorsal and ventral faces; in triticinoid genera compression lacking or lateral or somewhat dorsiventral; (3) caryopses with an open or wide sulcus in elymoid and henrardioid genera, narrow or closed in triticinoid; (4) hilum linear, often black or dark, lying in the sulcus, almost as long as caryopsis; (5) corona a thin membranous appendage, whitish, cream, or yellowish, flattened dorsiventrally and extending vertically above the

caryopsis apex, or in triticinoid genera covering the apex horizontally like a cap; (6) apical hairs borne on the corona, sparse to dense, short to long; corona and hairs usually 0.5–1 or 1.5 mm long, or hairs absent in certain species; (7) embryo (2/5–) 1/3–1/5 (–1/6) as long as caryopsis; (8) endosperm solid, but not very hard; (9) caryopses heteromorphic (varying in size or shape in one spikelet) in *Aegilops, Dasypyrum, Heteranthelium,* and perhaps *Triticum;* (10) two-branched style relatively short, usually broken off in mature caryopses; (11) embryo formula F + FF or F - FF (Reeder 1957); and (12) lemma and palea usually tightly attached to caryopsis.

Conclusions

The Triticeae can be divided into two major subtribes and one monogeneric subtribe (Table 3). The genera within the triticinoid group exhibit similar caryopses features among the species as do the genera in the elymoid group. The genera in these subtribes vary with the opinions of the botanists studying them (e.g., Runemark and Heneen, 1968; Sakamoto, 1973). Our opinion on the composition of these subtribes rests on our interpretations of the caryopsis morphology and the inclusion of other types of data.

The main differences between elymoid and triticinoid groups may be summarized in the form of a key:

TABLE 3.—Classification for genera examined. Nomenclatural citations follow Clayton and Renvoize (1986).

Tribe: TRITICEAE Dumortier, Obs. Gram. Belg. 82. 1824.
- Subtribe 1: TRITICINAE Grisebach, Fl. Rumel. Bithyn. 2:422. 1844.
  - Type: *Triticum* Linnaeus
  - Genera: *Aegilops*
    Amblyopyrum
    Dasypyrum
    Heteranthelium
    Secale
    Triticum
- Subtribe 2: HORDEINAE Dumortier, Obs. Gram. Belg. 91. 1824.
  - Type: *Hordeum* Linnaeus
  - Genera: *Agropyron*
    Crithopsis
    Elymus
    Elytrigia
    Eremopyrum
    Hordelymus
    Hordeum
    Leymus
    Psathyrostachys
    Taeniatherum
- Subtribe 3: HENRARDIINAE C.E. Hubbard in Hooker, Ic. Pl. 35. t. 3453. 1948.
  - Type: *Henrardia* C.E. Hubbard

Uncertain alignment: *Brachypodium*

Caryopses dorsiventrally compressed; often lanceolate, oblong, or oblanceolate; sulcus usually wide, occupying 1/2 or more of the ventral face or narrow at the base and widened distally; corona a short projecting appendage at apex of caryopses, often with dense, medium to long apical hairs; embryos often about 1/4 as long as caryopses . . . . . Elymoid Group

Caryopses not compressed (round in transverse section) or laterally compressed or dorsiventrally compressed only ventrally in *Aegilops* and *Amblyopyrum;* often ovate or elliptic; sulcus narrow or closed; corona covering the apex like a horizontally flattened cap, often with sparse hairs or lacking hairs; embryos often 1/3 as long as caryopses . . . . . Triticinoid Group

We conclude that non-embryo characters of the Triticeae provide significant systematic data. We establish the existence of two distinct groups of genera in the Triticeae, here recognized as subtribes Hordeinae and Triticinae (Table 3). Within the Hordeinae our data support a broad delimitation of *Elymus.*

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